REVISION AND CLADISTIC ANALYSIS OF THE ORBWEAVING SPIDER GENUS *CYRTOGNATHA* KEYSERLING, 1881 (ARANEAE, TETRAGNATHIDAE)

DIMITAR DIMITROV

Department of Biological Sciences
The George Washington University
Washington, D.C., 20052
(dimitard@gwu.edu)

GUSTAVO HORMIGA

Department of Biological Sciences
The George Washington University
Washington, D.C., 20052
and
Division of Invertebrate Zoology
American Museum of Natural History, New York
(hormiga@gwu.edu)

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ABSTRACT

The Neotropical spiders of the orbweaving genus *Cyrtognatha* Keyserling, 1881 (Tetragnathidae) are monographed. *Cyrtognatha* now includes a total of 21 species distributed over a large part of South America, Central America, and the southern parts of North America. Several species are known from the Caribbean islands of Cuba (one species), Hispaniola (two species), Jamaica (one species), and Saint Vincent (one species). Despite the wide geographic distribution of the genus, most *Cyrtognatha* species are known from single localities and often from very few museum specimens. The web architecture of several *Cyrtognatha* species is described and illustrated for the first time. Adults and juveniles of *Cyrtognatha* can be easily distinguished from all other tetragnathids by the presence of a straight line of long and robust macrosetae with enlarged bases on the retrolateral surface of the PLS. In *Cyrtognatha* the spermathecae are reduced and the sperm storage function is undertaken by an unpaired membranous structure, the posterior sac, which is diagnostic for the genus. A cladistic analysis including all known species of *Cyrtognatha* plus 51 outgroup taxa scored for a total of 194 morphological and behavioral characters was carried out. Thirteen unambiguous synapomorphies support the monophyly of *Cyrtognatha*, six of which are free of homoplasy. The internal phylogenetic relationships within the genus are also hypothesized and discussed. The genus *Agriognatha* O.P.-Cambridge, 1896 is a junior synonym of *Cyrtognatha*. The following eight new combinations are proposed: *C. pachygnathoides* (O.P.-Cambridge, 1894), *C. bella* (O.P.-Cambridge, 1896), *C. lepida* (O.P.-Cambridge, 1889), *C. simoni* (Bryant, 1940), *C. rucilla* (Bryant, 1945), *C. espanola* (Bryant, 1945), *C. bryantae* (Chickering, 1956), and *C. insolita* (Chickering, 1956). The following 11 new species are described: *C. catia*, n. sp., *C. atopica*, n. sp., *C. eberhardi*, n. sp., *C. quichua*, n. sp., *C. waorani*, n. sp., *C. morona*, n. sp., *C. leviorum*, n. sp., *C. petila*, n. sp., *C. paradoxa*, n. sp., *C. orphana*, n. sp., and *C. pathetica*, n. sp. The species *C. aproducta* Franganillo, 1926 is considered a nomen dubium. The following three new combinations are the result of generic misplacements: *Tetragnatha lactensis* (Mello-Leitão, 1947), *T. exilima* (Mello-Leitão, 1943), and *Glenognatha globosa* (Petrunkevitch, 1925).

INTRODUCTION

As circumscribed and revised in this monograph, the genus *Cyrtognatha* Keyserling, 1881 (figs. 1, 2) includes 21 species of tetragnathine spiders. More than half of the species are new to science and most of them are known only from a few museum specimens. This latter fact, in conjunction with the broad geographic distribution of the genus (from Argentina to Mexico), suggests that a significant fraction of the species diversity of *Cyrtognatha* remains undiscovered. Although described more than a century ago, the tetragnathid spider genera *Agriognatha* O. P.-Cambridge, 1896, and *Cyrtognatha*, have never been revised or studied in any detail. Prior to our work the only natural history information available for *Cyrtognatha* was limited to the museum specimen labels; no photographs of live animals were known to us and the web architecture remained a mystery. Before the present work the taxonomic status of these two generic concepts was far from clear. Originally, many of the species placed in *Agriognatha* were described in the genus *Cyrtognatha*. O. P.-Cambridge (1896) considered *Cyrtognatha* to be a junior homonym of the genus *Cyrtognathus* Falderman, 1835 (Coleoptera), and he erected the genus *Agriognatha* to solve this problem. However, Simon (1897) considered *Agriognatha* as a junior synonym of *Cyrtognatha*, arguing that *Cyrtognatha* and *Cyrtognathus* should not be treated as homonyms. In his catalog of American spiders, Petrunkevitch (1911) also listed *Agriognatha* as a junior synonym of *Cyrtognatha*.

Bryant (1940) acknowledged that *Agriognatha* and *Cyrtognatha* are actually the same genus but followed the decision of O. P.-Cambridge to treat *Cyrtognatha* as a homonym of *Cyrtognathus*. The opposite view was adopted by H. Levi, who followed Simon in using the name *Cyrtognatha*. *Agriognatha* does not appear in Levi's key to tetragnathid genera and he consistently uses *Cyrtognatha* instead (H. Levi, unpubl. key). To further complicate this situation, Chickering (1956a) considered *Agriognatha* and *Cyrtognatha* as

two separate genera, stating that there are characters that clearly separate them. Unfortunately, Chickering did not describe the alleged diagnostic characters.

Both genera were also listed as valid in the Platnick's spider catalog, which included a small disclaimer about known taxonomic issues (Platnick, 2006).

The present study is the first detailed taxonomic revision of these two genera. It aims to resolve the ongoing taxonomic argument about the circumscription of *Agriognatha* and *Cyrtognatha*. The study of type specimens and other museum material, as well as recently collected specimens, clearly suggests that *Agriognatha* is a junior synonym of *Cyrtognatha*. Furthermore, our study has resulted in a large increase in the species diversity of this lineage, with the addition of 11 new species. We also study, by the means of cladistic analysis, the species level phylogenetic relationships and the placement of the *Cyrtognatha* clade within Tetragnathidae.

Materials and Methods

Most of the specimens used for this study come from the museum collections listed at the end of this section. Additional specimens were collected during several trips by the second author in Costa Rica (1995), Ecuador (1996), and Colombia (1998); by G. Hormiga, F. Álvarez-Padilla, and S. Benjamin in the Dominican Republic (2005); and by F. Álvarez-Padilla and L. Lopardo in Mexico (2005). In several cases the web architecture was documented using Nikon F100, Nikon D200, and/or Nikon Coolpix 995 cameras. For photography, webs were dusted with cornstarch (Eberhard, 1976; Carico, 1977).

Morphological methods of study follow those previously described in Hormiga (1994, 2000). Specimens were examined and illustrated using Leica MZ16 and Leica MZ16A stereoscopic microscopes with a camera lucida. Further details were studied and depicted under a Leica DMRM compound microscope with a drawing tube. Drawings of the male palp and the female genitalia were done with graphite pencils on an acid-free cotton paper. Hairs and macrosetae are not depicted in the final drawings. For the male palp illustrations, the left palp was used unless otherwise stated (if the left palp was missing, the right one was used, and this is indicated in the legend of the corresponding figure). Female genitalia were dissected, and the nonchitinous abdominal tissue was digested with pancreatin enzyme complex (P1750 from Sigma-Aldrich; seeÁlvarez-Padilla and Hormiga, 2008). The pancreatin complex was diluted in a saturated solution of sodium borate prepared as described by Dingerkus and Uhler (1977). After removing any remaining tissues with needles, the preparations were washed in distilled water and transferred to 75% ethanol for observation and illustration. All pencil drawings were scanned and edited with the help of the program Gimp 2.2.10. Digital images of the specimens were taken using a Leica MZ16A stereoscopic microscope with a Nikon DXM1200F digital camera. Series of partially focused images were stacked with the Auto-Montage 4.02.0014 program to produce final images with enhanced quality.

The species for which enough specimens were available were also studied with a LEO 1430VP scanning electron microscope (SEM). For SEM, abdomen, legs, cephalothorax, and male palps were dissected and cleaned ultrasonically (up to 1 minute), transferred to 100% ethanol, and left to dehydrate for ca. 24 hours. After dehydration the specimens were critically point dried, mounted, and coated with gold-palladium for observation as described in Álvarez-Padilla and Hormiga (2008). The female internal genitalia and the tracheal system were cleaned and digested as described above (ultrasonic cleaning was not necessary).

All morphological measurements were taken with the help of scale reticle in the dissecting microscope. Morphological measurements in the text are in millimeters.

Abbreviations Used in Text and Figures

AC	aciniform gland spigots
Adt	distal tubercle of the abdomen
AG	aggregate gland spigots
ALE	anterior lateral eyes
ALS	anterior lateral spinnerets
AME	anterior median eyes
BH	basal hematodocha
BL	booklung

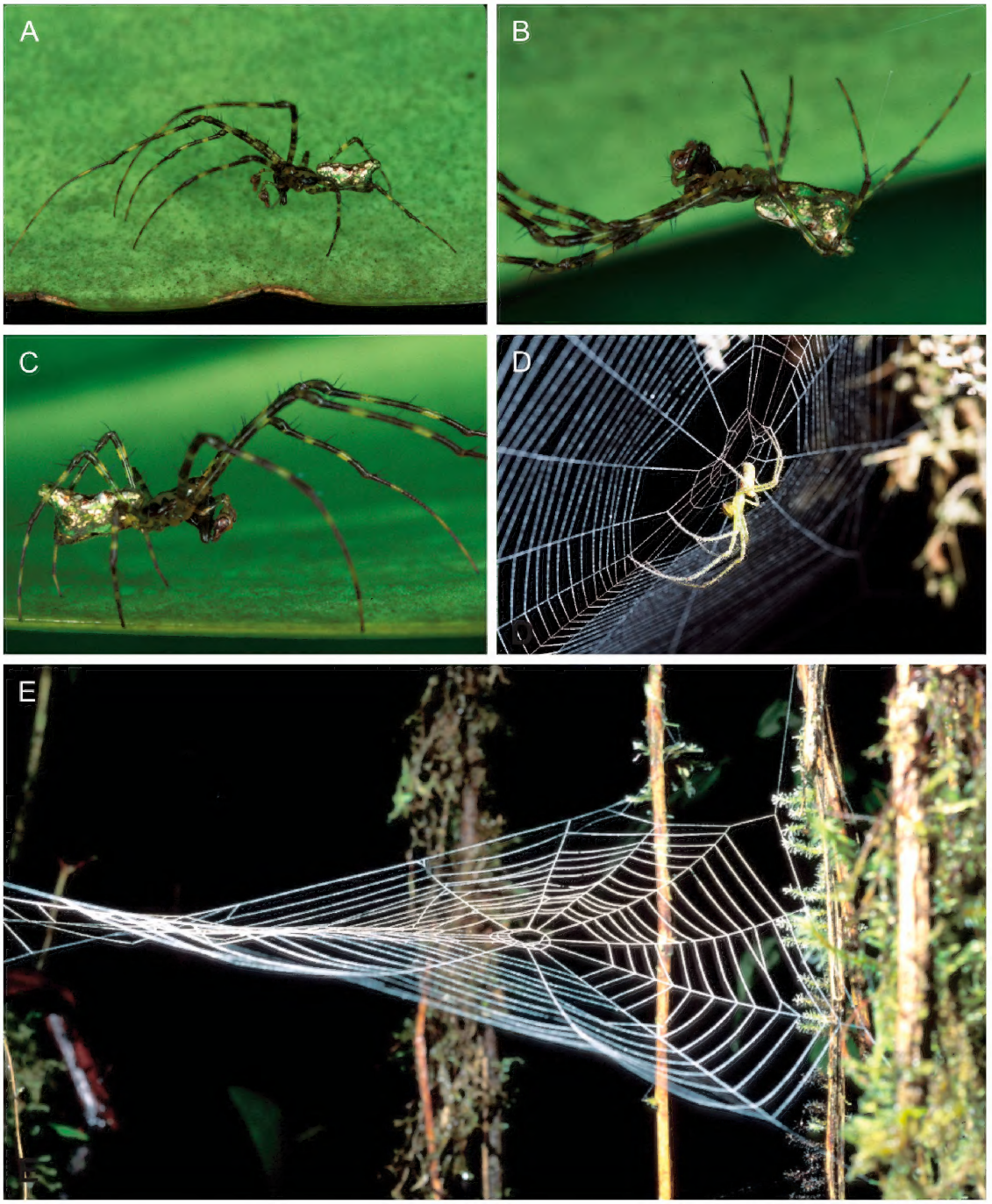

Fig. 1. Webs and habitus of *Cyrtognatha quichua* (from Ecuador, Sierra Azul). Habitus in vivo of *Cyrtognatha quichua* (**A–C**). Habitus in vivo of *Cyrtognatha rucilla* (**D**) (from Dominican Republic, Cachote). Web of *Cyrtognatha quichua* (**E**) (**E**, web diameter ca. 26 cm).

Fig. 2. Webs and web posture of *Cyrtognatha rucilla* (**A–E**) (from Dominican Republic, Cachote; B and E, web diameter ca. 12.5 cm), figure 2A is from Dimitrov et al. (2007: fig. 1). Web of *Cyrtognatha espanola* (**F**) (from Dominican Republic, Cachote; web diameter ca. 12.5 cm). White arrow shows drag line going out of the web.

C	conductor
CAp	conductor apical apophysis
CB	cymbium
CBa	conductor basal apophysis
CD	copulatory duct
Cdt	cheliceral dorsal tooth
CY	cylindrical gland spigots
E	embolus
EB	embolus base
Eba	embolic basal apophysis
ED	ejaculatory duct
ETm	embolus tegulum membrane
F	fundus
FL	flagelliform spigot
Lms	PLS line of macrosetae
MAf	metine embolic apophysis membranous fold
MAP	major ampullate gland spigot
mAP	minor ampullate gland spigot
MEA	metine embolic apophysis
MPT	most parsimonious tree
MS	median sac
P	paracymbium
PI	piriform gland spigots
PLE	posterior lateral eyes
PLS	posterior lateral spinnerets
PME	posterior median eyes
PMS	posterior median spinnerets
PS	posterior sac
S	spermatheca
ST	subtegulum
T	tegulum
UE	uterus externus

Museum Collections

AMNH	American Museum of Natural History, New York
BMNH	The Natural History Museum, London
CNAN	Colección Nacional de Arácnidos, Mexico, D.F.
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MIZ	Muzeum i Instytut Zoologii, Polska Akademia Nauk, Warsaw
MNHM	Muséum National d'Histoire Naturelle, Paris
MNRJ	Museo Nacional Universidade Federal do Rio de Janeiro, Rio de Janeiro
USNM	National Museum of Natural history, Smithsonian Institution, Washington, D.C.
YPM	Yale Peabody Museum of Natural History, New Haven, Conn.

PHYLOGENETICS

Taxonomic Sampling

All known species of *Cyrtognatha* and *Agriognatha* were included in the cladistic analyses. The rest of the taxa in the data matrix cover 25 of the 58 genera (including "Nephilidae") in the family Tetragnathidae, as well as several other closely related families. Outgroup taxa are as in the matrix of Álvarez-Padilla (2007).

Because *Tetragnatha* and *Cyrtognatha* are very similar and presumably closely related, we decided to include two more species of *Tetragnatha* Latreille, 1804 to the matrix in order to more rigorously test the monophyly of *Cyrtognatha*. These species were *Tetragnatha javana* (Thorell, 1890) (figs. 67–69) and *Tetragnatha* sp. (from the Dominican Republic, figs. 69–71). Each one of them exhibits a very different set of morphological characteristics (especially the females), with which, together with *T. versicolor* Walckenaer, 1842, we attempt to represent the morphological diversity of this genus (a modest attempt nonetheless, given the size of the genus). With the addition of these two species, a total of 72 taxa are included in the character matrix.

The main goal of our analyses is to reconstruct the species-level phylogenetic relationships within the genus *Cyrtognatha*. At first glance, using such a wide taxonomic sample might seem excessive for the species-level phylogeny. One might argue that since we know that the genus of interest falls in the subfamily Tetragnathinae, it is not necessary to include so many tetragnathid genera and representatives of other families in order to test its phylogenetic placement and monophyly. We decided to keep all taxa included in the original matrix for several reasons. Although the morphology of *Cyrtognatha* strongly suggests that the genus is a member of Tetragnathinae, the closest relatives of this

subfamily remain uncertain (but see Álvarez-Padilla, 2007). Choosing an outgroup within the family would be highly subjective and might seriously affect character optimizations in the ingroup. The inclusion of many tetragnathid taxa in the matrix should help us to gain a better understanding of character evolution and should provide a more rigorous test of the phylogenetic relationships.

The same six araneoid families included in the original matrix (Álvarez-Padilla, 2007) were used as outgroups (following Griswold et al., 1998) and the trees were rooted with *Uloborus* Latreille, 1806.

Characters

A large fraction of the characters used in this study were described and used in previous phylogenetic works on Tetragnathidae. The first 168 characters in the matrix are taken from the most recent phylogenetic analyses of this family by Álvarez-Padilla (2007) and Kuntner (2006). Characters 1–105 were taken from Álvarez-Padilla (2007) and characters 106–168 are taken from the matrix published in Kuntner (2006). Importantly, however, some of these characters were known and broadly discussed in previous papers, for example, Levi (1980), Coddington (1990), Hormiga et al. (1995), Scharff and Coddington (1997), Griswold et al. (1998), and Tanikawa (2001).

For most of the outgroup taxa the characters were coded as in the original matrices. In several cases new observations required recoding of some of the characters. Additionally, many characters present in Kuntner (2006) were not included in the analysis as such because they were already coded in Álvarez-Padilla (2007) (chars. 6, 16, 17, 33–35, 37, 43, 46–48, 50, 72, 75, 78, 99–108, 117, 122–124, 126, 128, 130, 133, 139, 142, 143, 154–157, 159–161, 166, 172, 174, 175, 177–179, 182, 183, 185–187, and 189). Differences in the taxonomic sampling of Kuntner (2006) rendered several characters uninformative and therefore those were excluded from our matrix (chars. 3, 5, 7–9, 42, 44, 45, 53, 54, 56, 65, 77, 79, 87, 88, 90, 97, 98, 120, 135–138, 158, 166, 168, 169, and 184). In some cases published character definitions were unworkable and it was impossible to replicate state assignments across taxa in the original matrix (e.g., char. 10 in Kuntner, 2006) or it was not possible to objectively distinguish the states of a character. For example, characters 58–64 in Kuntner (2006) refer to cuticular sclerotizations in the abdomen, but the absence of sclerotizations needs to be verified with SEM. In *Dolichognatha* O. P.-Cambridge, 1869, and *Azilia* Keyserling, 1881, the ventral sclerotizations cannot be seen with the stereoscope, but are visible, although small, under SEM (F. Álvarez-Padilla, personal commun.). As a consequence, the following characters from Kuntner (2006) were not included: 1, 4, 9–12, 20, 23, 30, 40, 41, 49, 52, 58–64, 66–70, 76, 80–83, 93, 114, 131, 162, and 188.

The so-called "embolic conductor" (EC) and all characters describing it in Kuntner (2006) are not included as such. We disagree with the statement that the embolic conductor is a novel sclerite as proposed by Kuntner (2005, 2006). According to Kuntner, the main reason to call this palpal sclerite an embolic conductor not homologous to the araneoid conductor itself is the presence of a membrane that connects the embolic conductor with the embolus membrane and the tegulum. However, there are several tetragnathid genera that have a membranous attachment of the conductor to the tegulum (e.g., *Leucauge* White, 1841, and *Cyrtognatha*). At least in three species of *Leucauge* that we have examined (*L. venusta* (Walckenaer, 1842), *L. mariana* (Taczanowski, 1881), and *L. argyra* (Walckenaer, 1842)) the conductor and the embolus are attached to the tegulum with a joint membrane. This is identical to the condition described for nephilines and might be interpreted the same way, but it is coded differently in the matrix of Kuntner (2006)—"nephilids" as having the embolic conductor (but lacking the araneoid conductor) and *Leucauge* as lacking the embolic conductor but having instead the araneoid conductor. We think that in both cases ("nephilids" and other tetragnathids) this tegular sclerite should be interpreted as homologous to the araneoid conductor, and it has been coded as such in our character matrix.

Changes to the character coding based on the examination of additional specimens and/

or illustrations and photographs of webs are as follows:

Character 4. Position of the tracheal spiracle. Previously coded as advanced (Hormiga et al., 1995; Álvarez-Padilla, 2007) for *Pachygnatha* Sundevall, 1823. According to our observations, it is not advanced but is very close to the spinnerets (most probably it was confused with the genital opening in previous studies). Accordingly, *Pachygnatha* was changed to state 0 (posterior).

Character 33. Sustentaculum. Coded as absent in nephilines in several studies (Hormiga et al., 1995; Griswold el al., 1998; Álvarez-Padilla, 2007), but Kuntner (2005, 2006) considered it present in all nephilines. After examining the available SEMs of nephilines (Kuntner, 2005, 2006) we agree with the decision of Kuntner (2005, 2006), and the substentaculum is coded as present for nephilines in our matrix.

Character 50. Articulated paracymbium. Previously coded as integral (1) for the genus *Agriognatha* (Álvarez-Padilla, 2007), but observations of the expanded male palps show that it is actually articulated although it is not a separate sclerite. The state was changed to 3 (articulated) accordingly.

Character 107. Posterior eye row. This corresponds to character 13 in Kuntner (2006). After examining specimens of *Epeirotypus brevipes* O. P.-Cambridge, 1894 (Theridiosomatidae), we consider that it should be coded as 0 (straight to recurved). The original coding of 1 (procurved) was changed to 0 in the matrix.

Character 108. Female PME. This character corresponds to character 14 in Kuntner (2006) where *Epeirotypus brevipes* was coded as 1 (one or more than one PME diameter apart). After examining specimens from this species we conclude that it should be coded as 0 (less than one PME diameter apart) and the matrix was changed accordingly.

Character 114. Female sternal tubercle II. Corresponds to character 26 in Kuntner (2006). *Metellina curtisi* (McCook, 1894) was coded as 0 (absent) in Kuntner (2006). Here we recoded it as 1 (present) after examining several specimens.

Character 115. Female sternal tubercle III. Corresponds to character 27 in Kuntner (2006). *Metellina curtisi* recoded to 1 (present).

Character 116. Female sternal tubercle IV. Corresponds to character 28 in Kuntner (2006). *Metellina curtisi* and *Phonognatha graeffei* (Keyserling, 1865) are recoded to 1 (present). *Clitaetra episinoides* Simon, 1889 recoded to 0 (absent).

Character 117. Female frontal sternal tubercle. Corresponds to character 29 in Kuntner (2006). *Araneus marmoreus* Clerck, 1757 (Araneidae), has a frontal tubercle. Kuntner (2005, 2006) coded *Araneus diadematus* Clerck, 1757, and thus this difference in the coding may be the result of interspecific variation.

Character 118. Female chilum. Corresponds to character 31 in Kuntner (2006). After specimen examination, two taxa needed to be recoded: *Nesticus cellulanus* (Clerck, 1757) (Nesticidae) and *Steatoda americana* (Emerton, 1882) (Theridiidae) were both found to have a chilum.

Character 119. Female chelicerae. Corresponds to character 32 in Kuntner (2006). *Argiope argentata* (Fabricius, 1775), *Metellina curtisi*, and *Pachygnatha autumnalis* Marx, 1884 were recoded as 1 (slender).

Character 122. Femoral macrosetae. This character was first described by Griswold et al. (1998), and since then it has been widely used in phylogenetic analyses of araneoid relationships. Kuntner (2005, 2006) coded *Phonognatha graeffei* as lacking macrosetae on the first femur, but we have found that macrosetae are present and in our matrix the coding is changed to 1 (present).

Character 124. Female ventromedian sclerotizations. This character corresponds to the character 57 in Kuntner (2006). Two taxa are coded differently according to our observations. These are *Clitaetra episinoides* (coded as absent) and *Tetragnatha versicolor* (coded as absent).

Character 125. Female abdominal sigillae. In Kuntner (2005, 2006) this character referred to sclerotizations different from the classical dorsal sigillae. We have redefined it as the dorsal sigillae. This term was used in the literature to specifically denominate the dorsal sclerotized apodemes of the muscles attaching the heart to the cuticle. The use of the same term to denominate other structures might lead to confusion and should be avoided. Here, as in most of the characters

that refer to apodemes on the cuticle, it is important to note that most spiders may have the same apodemes but with different degrees of sclerotization. SEM images show that some spiders that do not have sclerotized apodemes visible under stereomicroscope have clearly distinguishable apodemes when observed under SEM. As a result, when coding such sclerotizations what is being coded is not the presence or absence of apodemes but the degree of their sclerotization.

Character 126. Female abdomen tip color. Corresponds to character 71 in Kuntner (2006). We recoded *Uloborus glomosus* (Walckenaer, 1842) (Uloboridae) as 1 (paired white dots around the spinnerets).

Character 127. Female venter light pigmented pattern. Corresponds to character 74 in Kuntner (2006). *Nephila clavipes* (Linnaeus, 1767) was recoded as 0 (one central white area).

Character 132. Copulatory opening form. Corresponds to character 91 in Kuntner (2006). Several taxa were recoded (*Leucauge venusta*, *Meta menardi* (Latreille, 1804), *Metabus ocellatus*, *Metellina curtisi*) according to our observations.

Character 133. Copulatory duct morphology. Corresponds to character 92 in Kuntner (2006). The coding for *Meta menardi* and *Metellina curtisi* was changed to 2 (broad attachment to body wall).

Character 139. Male vs. female cheliceral size. Corresponds to character 111 in Kuntner (2006). We have examined various specimens (males and females) of *Phonognatha graeffei* originating from different populations. In all cases we found that the males have larger chelicerae, and thus the coding of this character was changed to 1 (larger).

Character 144. Cymbium ectal margin. Corresponds to character 125 in Kuntner (2006). *Epeirotypus brevipes* was recoded as 1 (transparent) and *Phonognatha graeffei* was recoded as 0 (sclerotized as cymbium). The male palp of *Phonognatha graeffei* has a transparent structure in ectal view, but in this species this structure is homologized to the paracymbium (Hormiga et al., 1995).

Character 145. Paracymbium setae. Corresponds to character 125 in Kuntner (2006). We examined specimens of *Herennia multipuncta* (Doleschall, 1859) and found setae on the paracymbium, and thus this species was recoded accordingly.

Character 148. Tegulum in ectal view. Corresponds to character 129 in Kuntner (2006). *Araneus marmoreus* was coded as 0 (same size or larger than subtegulum). In Kuntner (2006) *Araneus diadematus* Clerck, 1757, was coded as 1 (smaller than the subtegulum); however, here we used different species of *Araneus*, so this difference might be a result of variation between species. *Argiope argentata* was also changed to 0 (1 in Kuntner, 2006). Nonetheless, it is difficult sometimes to decide the state assignment depending on the orientation of the palp sclerites.

Character 149. Ejaculatory duct path. Corresponds to character 132 in Kuntner (2006) where *Tetragnatha versicolor* was coded as 1 (joints distally the embolus). We have examined specimens of *Tetragnatha versicolor* as well as several other species (*T. javana*, *T. guatemalensis* O. P.-Cambridge, 1889, and *Tetragnatha* sp. from the Dominican Republic) of the same genus, and in all of them the ejaculatory duct enters the embolus in its base. All *Tetragnatha* species are coded here as 0 (within the entire length of the embolus).

Character 153. Embolus length. Corresponds to character 153 in Kuntner (2006). We consider that *Nesticus cellulanus* and *Pimoa altioculata* (Keyserling, 1886) (Pimoidae) have short emboli (less than half of the cymbium length) and we recoded them accordingly. Additionally, the definition for the state 0 was changed from "more than twice the cymbium length" to "more than 1.5 times the cymbium length". In the original definition of the states of this character (Kuntner, 2005) there is a gap between the state 0 (more than twice the cymbium length) and the state 1 (between 0.5 and 1.5 times the cymbium length).

Character 166. Partial web renewal. Corresponds to character 195 in Kuntner (2006). *Nesticus cellulanus* was coded as 0 (absent) in Kuntner (2006). Here changed to 1 (present) (S. Benjamin, personal commun.).

To resolve the phylogenetic relations of *Cyrtognatha*, 26 new characters (169–194)

were defined and added to the matrix. The following is the complete list of these characters together with their definitions.

169. Line of macrosetae on the retrolateral surface of the PLS (e.g., figs. 28G, 28J, 35E). (0) some setae may be present but they do not form such line; (1) well-developed macrosetae with enlarged bases and arranged in a straight line. All specimens of *Cyrtognatha* that we examined had such arrangement of macrosetae on the PLS. This character is an autapomorphy for *Cyrtognatha* and is one of the important diagnostic characters for this genus.

170. Male chelicerae orientation. (0) not projected (fig. 1A, C); (1) projected (see *Tetragnatha*). This character refers to the orientation of the male chelicerae with respect to the cephalothorax. In some species the male chelicerae are projected with respect to the cephalothorax (e.g., *Tetragnatha*). One important problem for the correct coding of this character is the possible changes of the orientation of the chelicerae due to the dehydration effect of the alcohol. When it is suspected that such effect may have taken place, the best solution is to observe live animals in order to code them.

171. Male chelicerae divergence. (0) not divergent—the lateral distal axis of the chelicerae is on a line, which is almost parallel to the central axis of the chelicerae (fig. 4E); (1) moderately divergent—this line is forming an angle with the central axis of the chelicerae and this angle is less than 45° (fig. 4C); (2) widely divergent—the angle formed between these two lines is more than 45° (in some species it is close to 90°) (fig. 4D).

172. Male cheliceral dorsal tooth. (0) absent; (1) present (figs. 12E, 42E, 53B, D). In some genera (e.g., *Tetragnatha*; see fig. 67F, G) there is often more than one dorsal tooth on the male chelicerae. However, it is not difficult to establish the homology for it, as the dorsal tooth is always much stronger, closer to the fang articulation, and it often has short outgrowths apically.

173. Male cheliceral dorsal tooth position relative to the fang articulation. (0) close to the fang articulation (fig. 42E); (1) outlying the fang articulation (fig. 9E). In some species of *Cyrtognatha* and also in most of the *Tetragnatha* the dorsal tooth is placed relatively far from the fang articulation (this is especially pronounced in some *Tetragnatha* species, such as *T. javana*).

174. Male cheliceral fang outgrowth. (0) fang without outgrowth (fig. 38B, F); (1) with well-developed outgrowth (fig. 42B, E). This character refers to the presence of a small, usually sharpened, dorsal outgrowth of the male cheliceral fang. Many tetragnathines have a similar structure of the male fang, and it is also present in most of the *Cyrtognatha* species.

175. Cymbium/tibia proportion. (0) long tibia (cymbium/tibia less than 2.8); (1) short tibia (cymbium/tibia more than 2.8). In some *Cyrtognatha* species the tibia of the male palp is much longer than in other congeners. We measured the cymbium/tibia proportion in at least one male of each species and in three males of the species where more specimens were available. Based on these measurements all species were divided into two groups, in which this proportion shows continuous variation. However, there is a small gap between these species ratios and there were not specimens of either group with a proportion of 2.8. Thus, this value was chosen to separate the two states.

176. Apical embolus membrane. (0) absent; (1) present (fig. 20B, C). Some species of *Cyrtognatha* have a translucent membranous ridge on the embolus. This membrane ranges from just a small structure near its tip (*C. insolita*) to a more complex structure with a more chitinized basal part (*C. paradoxa*, n. sp.).

177. Embolus enlarged ventrally. This character refers to the conspicuously widened embolus observed in some species of *Cyrtognatha* (e.g., *C. insolita*). (0) embolus with a conspicuously enlarged portion (figs. 37A, 39E, H); (1) embolus without apparent enlargement (fig. 10B, C). The embolus in all *Cyrtognatha* species is enlarged in comparison to the other members of the subfamily. However, in several species it has a conspicuously enlarged part that often is more than twice the width of the rest of the embolus. The portion of the spermatic duct that passes through this enlarged section is not significantly enlarged in most of the cases. For example, *C. nigrovittata* has an

enlarged embolus but the spermatic duct is not enlarged, while in *C. morona*, n. sp., the spermatic duct also enlarges.

178. Apical embolus membrane extension. (0) extension does not reach the tip of the embolus (fig. 17A–C); (1) extension reaches to the tip of the embolus (fig. 8A, B). When apical embolus membrane is present in some species it reaches to the tip of the embolus, while in other congeners it ends before its apical part.

179. Embolus tip turnover. (0) absent (fig. 17A–C); (1) present (figs. 41E, 43G). This character refers to the conspicuous embolus subapical turnover found in several *Cyrtognatha* species from the Antilles and Central America (e.g., *C. rucilla*).

180. Embolus basal apophysis. (0) absent; (1) present (fig. 9A, B). This character refers to the presence of a small apophysis near the base of the embolus in some species (e.g., *C. atopica*, n. sp.). This apophysis does not form part of the MEA and it is placed very close to the base of the embolus. The base of the embolus of many tetragnathids, especially those within leucaugines, may have a different apophysis (Álvarez-Padilla, 2007). The diverse position and morphology of these apophyses adds considerable difficulty to homology interpretations. The emboli in *Metellina* Chamberlin and Ivie, 1941, and in *Dolichognatha* carry an embolic apophysis that has a rigid connection to the embolus, while in *Allende* Álvarez-Padilla, 2007, it is membranous (Álvarez-Padilla, 2007). The basal apophyses found in *Cyrtognatha* are very characteristic structures similar to a small ridge near the base of the embolus. They are easily distinguishable from basal embolic apophyses in other tetragnathids and are coded in this character as non-homologues to the balas embolic apophyses in other tetragnathids.

181. Conductor basal apophysis. (0) absent; (1) present (figs. 9A, 13I). All *Cyrtognatha* species and some outgroup taxa (e.g., *Glenognatha* Simon, 1887) have a basal apophysis of the conductor that starts near its base and runs under the embolus.

182. Conductor basal apophysis membrane. (0) basal apophysis narrower distally and without or with very small membrane distally (fig. 43G); (1) basal apophysis with a well-developed transparent membrane distally (fig. 10C); (2) basal apophysis widened distally and without or with very small transparent membrane (fig. 17A). The tip of the basal apophysis of the conductor is variable within *Cyrtognatha* and proves to be a very useful character for the species determination and phylogenetic reconstruction.

183. Conductor apical apophysis. (0) absent; (1) present (figs. 17A, 27A). This character refers to the conspicuous nearly triangular apophysis of the conductor present in *Cyrtognatha*, easily observed in ventral view. In many tetragnathids the conductor carries apophyses that often are difficult to homologize. However, the apophysis of *Cyrtognatha* has a very characteristic shape and position relative to the other sclerites of the bulb (fig. 6C–E). Its morphology is very similar among the *Cyrtognatha* species and very different to the conductor apophyses observed in other genera like *Tetragnatha* or *Allende*.

184. Embolus serrated membrane. (0) absent; (1) present (fig. 39A, B, I). This character refers to the presence of a characteristic membrane on the embolic surface facing the MEA in several *Cyrtognatha* species. This membrane is covered with numerous tiny outgrowths, which give it a serrated appearance under the light microscope. None of the other tetragnathids or araneoid out-groups studied here have similar structure.

185. MEA prolateral fold. (0) absent (fig. 41A); (1) present (figs. 25A, 27A). The MEA of many *Cyrtognatha* species is very well developed and highly modified. In some species it has a more chitinized basal part, which carries a big folded membrane between the MEA and the embolus (fig. 13A).

186. Spermathecae development. (0) spermathecae well developed; (1) spermathecae absent (figs. 31D, E, 34B–E). The absence of spermathecae and the development of a specialized compartment of the median membranous chamber of the vulva, a posterior sac that stores the sperm, is an autapomorphy of *Cyrtognatha* (Dimitrov et al., 2007). A similar structure is found in some *Tetragnatha* species (fig. 64A; see also figures in Dimitrov et al., 2007), but all of them have very well-

developed spermathecae and a very small posterior sac. The posterior sac in *Tetragnatha* does not seem to store sperm, and its cuticle lacks the short stem gland ductules found in *Cyrtognatha*. See also characters 189 and 190.

187. Median sac of the vulva. (0) absent (figs. 7A, B, 40D, E); (1) present (figs. 7C, D, 34B). Several *Cyrtognatha* species have an additional compartment of the female genitalia, the median sac, which connects to the posterior sac and is placed anteriorly to it (Dimitrov et al., 2007). The median sac has a smooth cuticle, but in some cases small quantities of spermlike mass were observed inside it (fig. 31D).

188. Uterus externus connecting with the rest of the female genital apparatus via wide membranous saclike chamber. (0) absent; (1) present (figs. 7A–D, 40D, E). Such membranous chamber (Dimitrov et al., 2007) is found in all Tetragnathinae genera but not in *Diphya* Nicolet, 1849. The cuticle of this chamber and the rest of the uterus externus do not carry sclerotized gland ductules.

189. Posterior sac of the vulva. (0) absent; (1) present (figs. 7A–E, 40D, E).

190. Posterior sac with glands and modified for storing the sperm. (0) absent; (1) present (figs. 40D, E, 44D, E, 44J). In all *Cyrtognatha* species the spermathecae are strongly reduced and the posterior sac of the vulva is enlarged and contains a spermlike mass (Dimitrov et al., 2007). The cuticle of the posterior sac in *Cyrtognatha* also has numerous short gland ductules evenly distributed over its surface (fig. 44J). *Tetragnatha* species also have a posterior sac, but it is always very small and without ductules and the sperm is stored in well-developed spermathecae.

191. Distal tubercle of the male abdomen. (0) very small or absent (fig. 58C); (1) well developed—equal to or more than one third of the abdomen height at its distal edge (fig. 1A–C). Most *Cyrtognatha* species and many *Tetragnatha* have a well-developed distal tubercle on the abdomen.

192. Orientation of the distal tubercle of the male abdomen. (0) vertical (fig. 1A–C); (1) longitudinal (fig. 63B, C). The size of the distal tubercle of the male tubercle may vary between different specimens of the same species but not its orientation, which is either vertical (and inclined to some degree) or caudal.

193. Tip of the basal apophysis of the conductor. (0) continuous (fig. 60C); (1) with outgrowths (fig. 10C). The basal region of the conductor in some *Cyrtognatha* is a very complex structure and may carry several outgrowths.

194. Female fovea pits. (0) absent (fig. 46C); (1) present (fig. 68E). This character refers to the presence of well-delimited pits of the fovea on the male and female sternum. It is present in *Tetragnatha* and most of the leucaugines.

The full matrix is presented in appendix 1. The character matrix was built and edited with Mesquite version 1.06 (Maddison and Maddison, 2005).

Cladistic Analysis

Parsimony analyses were conducted with the software package TNT version 1.0 (Goloboff et al., 2003a) using a "traditional search" with 1000 replicates and the TBR swapping algorithm. Ten trees per iteration were kept. Minimum length = 0 (the default in TNT) was used as a collapsing rule in all searches. Cladogram manipulation and character optimizations were performed using TNT version 1.0 and WinClada version 1.00.08 (Nixon, 2002). All multistate characters were treated as nonadditive (Fitch, 1971).

Sensitivity Analysis (Assessing the Stability of the Optimal Trees)

Two different strategies were applied to assess the stability of the cladistic results. First, we used sampling-based techniques, namely bootstrap and jackknife. In both cases characters are randomly resampled and reweighted, and therefore the results of these tests can be taken as a good estimation for the sensitivity to random data perturbations. Although very similar, these two methods show several important differences. Bootstrap (Felsenstein, 1985) resamples characters and builds a matrix the same size as the original one. In this process characters are reweighted and character replacement is allowed. Jackknife (Farris et al., 1996) does

the same, but character replacement does not occur. Both bootstrap and jackknife were calculated as implemented in TNT performing 1000 replicates with removal probability for the jackknife set to 40%.

In addition to the standard bootstrap and jackknife, a Poisson weighting bootstrap and symmetric resampling (Goloboff et al., 2003b) were used. Both methods try to avoid the appearance of groups with high support in the results, which are actually not supported by the original data. The Poisson weighting bootstrap and the symmetric resampling analyses were carried out in TNT performing 1000 iterations and using 40% change probability with the symmetric resampling.

The other group of methods to assess clade support involves several strategies of character weighting. The idea to differentially treat characters is very old and can be traced back to Darwin (1859), who proposed that "conservative" characters should receive higher weight. However, choosing the character weights in an objective manner is not easy and has always been of great concern to systematists. We used two different methods of character weighting: successive approximations and implied weighting. Successive weighting (Farris, 1969; Carpenter, 1988) was performed as implemented in NONA version 2.0 (Goloboff, 1993a) by running the macro SWT.RUN. This implementation of the method uses the consistency index (CI) to reweight characters. The arguments used to run the program were "run swt.run hold10000 hold/10 mult*1000 jump50;".

Implied weighting analyses were conducted in TNT version 1.0. Under implied weighting, characters are treated differentially based on the degree of homoplasy, which they show in an individual tree (Goloboff, 1993b). One of the main differences with successive weighing is that under implied weights analsysis an optimality criterion (maximum fit) is provided to simultaneously weight characters and search for optimal tress. Existing character conflicts are resolved in favor of the characters with lower homoplasy by searching trees with a maximum total fit (Goloboff, 1993b). The fit is calculated as a concavity function, which depends on a concavity constant (K). As the values of K decrease, the weight of the characters with homoplasy drops. The value of K, however, still must be arbitrarily assigned. It is well known that with the increase of K the weighting against homoplasy decreases (this is, of course, by design of the weighting function) and at some point results start to converge to those from equal weights parsimony. However, this point is dependent on the data, and thus the only way to find it is to investigate a wide range of K values. As a result of the concave nature of the fit function, changes from one value to another in the lower limit of K are harsher, and therefore we have sampled more densely in this region.

Bremer Support

The original idea to use such approximation was proposed by Farris et al. (1982) for distance analyses and later by Bremer (1988) for parsimony. In the literature it is referred to also as "branch support" (Bremer, 1988, 1994), "Bremer support" (Källersjö et al., 1992), "decay index" (Olmstead et al., 1993), or "length difference" (Faith, 1991).

This method uses a profoundly different approach to access the branch support. It is based on the use of all original data without resampling, and the number of extra steps needed to lose a group in near-parsimonious trees is used as a measure for the branch support. This permits calculation of support values even in cases where resampling methods give very low support. Such situations are fairly common when analyzing morphological data, which makes the Bremer support a very commonly used clade support measure. Bremer support values were calculated using TNT.

Taxon Removal

Often the data matrices used for cladistic analyses contain high proportions of missing data. It has been demonstrated that highly incomplete information for a given taxon may influence negatively the accuracy of the phylogenetic analyses (Gauthier, 1986; Novacek, 1992; Wilkinson and Benton, 1995; Gao and Norell, 1998). We used the percentage of missing data as a criterion for

TABLE 1
List of Matrices Used in the Analysis with the Corresponding Excluded Taxa.

Species Excluded	Matrix Name
None	Complete
Ch. levii, *Ch. maitae*, and *C. lepida*	m_noCh_noLep
Ch. levii, *Ch. maitae*, and *C. pathetica*	m_noCh_noPat
Ch. levii, *Ch. maitae*, *C. lepida*, and *C. pathetica*	m_noCh_noLepPat

excluding taxa from the analsysis to evaluate their effect in the cladistic results. Two *Cyrtognatha* species in our data matrix have very high levels of missing data, *C. pathetica*, n. sp. (61.85%), and *C. lepida* (60.30%), both known only from female specimens. Furthermore, the very limited number of individuals available for study from these two species prevents us from using SEM, thereby creating additional difficulties for the coding of many ultrastructural characters. From the outgroup taxa the species with the highest proportion of missing data were *Chrysometa maitae* Álvarez-Padilla, 2007 and *Chrysometa levii* Álvarez-Padilla, 2007, with 67.52% and 54.12% of missing data, respectively. The two *Chrysometa* Simon, 1894, species were excluded from the analysis in combination with *C. lepida* or *C. pathetica* or with both *C. lepida* and *C. pathetica*. The resulting four character matrices have been labeled as follows (see also table 1):

Complete	All taxa included
m_noCh_noLep	*Chrysometa levii*, *Ch. maitae*, and *Cyrtognatha lepida* are excluded
m_noCh_noPat	*Chrysometa levii*, *Ch. maitae*, and *Cyrtognatha pathetica* are excluded
m_noCh_noLepPat	*Chrysometa levii*, *Ch. maitae*, *Cyrtognatha lepida*, and *C. pathetica* are excluded

RESULTS FROM THE CLADISTIC ANALYSIS

Complete Matrix. Equal weights parsimony analysis of the complete matrix finds 180 cladograms of minimal length (L = 719 steps, CI = 34.4, and RI = 74.4). From these, only 74 are valid, as the rest are reported as suboptimal after collapsing of all ambiguously supported branches. The strict consensus of these 74 MPTs (fig. 72) is 767 steps long (CI = 32.2 and RI = 71.8). If the same matrix is analyzed using the same search strategy but holding many more trees at each step (100–300 instead of the default 10), the analysis results in 282 trees, 99 of which are left after removing the suboptimal topologies. The consensus in both cases has the same topology. This behavior is clearly a result of the high proportion of missing data presented in the complete matrix. With the decreasing of the proportion of missing data, both strategies converge to the same results, and for the matrices m_noCh_noLep and m_noCh_noPat_noLep results are identical in both cases. Almost all topological differences between the most parsimonious trees are the result of different hypotheses of relationships within *Cyrtognatha*. In the strict consensus these relationships are almost fully unresolved, and most *Cyrtognatha* species, including the ones formerly placed in *Agriognatha*, form a polytomy. There is only one monophyletic group within *Cyrtognatha* formed by the Caribbean Islands endemics without *C. bryantae*. Despite the conflicting resolution of relationships within *Cyrtognatha*, the genus is always recognized as a monophyletic group and receives a very high support from all criteria applied. *Diphya* appears as a basal member of the subfamily Tetragnathinae, but this placement is weakly supported. The genus *Tetragnatha* appears as the sister group of *Cyrtognatha*.

Tetragnathidae is monophyletic but it is not supported by the indices based on resampling and shows very low Bremer support (2). Six main clades within Tetragnathidae can be defined: "Nephilidae" (including *Phonognatha* Simon, 1894), Tetragnathinae, Leucaugines (see Álvarez-Padilla, 2007), and three lineages of the genera formerly placed in the Metinae sensu stricto group (Álvarez-Padilla, 2007). One of these "metine lineages" is composed solely of the genus *Mollemeta* Álvarez-Padilla, 2007 and occupies a basal position in the sister clade to "nephilids".

The analysis of the complete matrix under successive weighting stabilizes after the second iteration and results in 94 trees (L = 723 steps, CI = 34, RI = 74). The strict consensus

of these trees is shown in figure 73A (L = 768 steps, CI = 32, RI = 71). None of these topologies is identical to those resulting from the equal weights parsimony analysis (the successive weighting cladograms are four steps longer than under equal weights). Nonetheless, the arrangement of outgroups is the same as in the MPTs resulting from the equal weights parsimony analysis. Tetragnathids are monophyletic and include "Nephilids" as the basal lineage. As under equal weights, *Phonognatha* is sister to the remaining "nephilids". In the strict consensus cladogram, *Cyrtognatha* species again form a polytomy with just four species (*C. espanola*, *C. rucilla*, *C. serrata*, and *C. simoni*) forming a monophyletic group. The main difference between the MPTs resulting from successive weighting and from the equally weighted parsimony analyses refers to the arrangement of the three main lineages of Metinae sensu stricto genera. Under successive weighting, Metinae sensu stricto forms a monophyletic group sister to leucaugines plus tetragnathines.

Implied weighting analyses always recovered *Cyrtognatha* as monophyletic, and within this clade the island endemic species (except for *C. bryantae*) are always a monophyletic group. For *K* values between 1 and 6 this latter group includes also *C. pachygnathoides*. For values of *K* greater than 6, the topology of the *Cyrtognatha* clade is identical to the one obtained with equal weights and under successive character weighting.

The relationships of the outgroup taxa changed significantly when using low values of *K* (1–6). When *K* = 1, *Mollemeta* becomes a basal member of the "nephilids". *Tetragnatha* turns polyphyletic with respect to *Glenognatha* and *Pachygnatha* for *K* = 1–2. *Chrysometa maitae*, *Chrysometa acinosa*, *Dolichognatha*, and *Diphya* also show very unstable behavior *K* values between 2 and 6.

For *K* = 9–25, the topology of the strict consensus cladograms is almost identical to the one obtained with successive weighting. The only difference is the arrangement of the taxa in the Metinae sensu stricto clade where *Dolichognatha* forms a monophyletic group together with *Meta* and *Metellina*. *K* values greater than 25 produce the same topology as that under equal weights. Analyses with *K* = 7–8 recovered the monophyly of the tetragnathids (with "nephilids" as most basal tetragnathid lineage) but placed *Dolichognatha* as sister to all other tetragnathids except the "nephilids". Statistics for all analyses are given in table 2.

M_NOCH_NOPAT MATRIX. Under equal weights the parsimony analysis results in 40 MPTs (L = 718 steps, CI = 34.4, RI = 74.5). Twenty of these trees were reported as suboptimal and were deleted; the strict consensus of the remaining trees is presented in figure 73B (L = 758 steps, CI = 32.6, RI = 72.3). The results are almost the same as those resulting from the analysis of the complete matrix. The only difference is the inclusion of *C. bryantae* and *C. bella* as basal members of the Caribbean Islands *Cyrtognatha* species clade. The groups that receive support values greater than 50 from the resampling methods are the same as in the analyses of the complete matrix. The only difference is the group *C. espanola* + *C. rucilla* + *C. serrata* + *C. simoni*, which here obtains low support values (between 54 and 58 depending of the method used). The results from the successive and implied weighting also closely resemble the results from the analyses of the complete matrix. None of the analyses of this matrix succeeds in unambiguously resolving the relationships between the different *Cyrtognatha* species.

M_NOCH_NOLEP MATRIX. Under equal weights the parsimony analysis results in eight optimal trees (L = 718 steps, CI=34.4, RI = 74), two of which were suboptimal and excluded from the consensus. The strict consensus of the remaining six trees is presented in figure 74 (L = 731 steps, CI = 33.8, RI = 72). The difference in the number of trees with respect to the m_noCh_noPat matrix is due to the more resolved relationships within the *Cyrtognatha* clade. Relationships among the outgroup taxa are as found in the previously described equal weights analysis. *Cyrtognatha* species together with the species formerly placed in *Agriognatha* form a monophyletic group. Within this group several clades can be defined. The Mexican species *C. paradoxa*, n. sp., occupies the most basal position with respect to all other *Cyrtognatha* species. *C. quichua*, n. sp.,

TABLE 2
Statistics for the Cladistic Analysis
(MP, maximum parsimony; SW, successive weighting; N, number of most parsimonious trees; L, tree length; F, tree fit. Number of trees excluding suboptimal topologies after collapsing ambiguously supported branches are in boldface type.)

	MP		SW		Value of *K*															
					1		2		3		4		5		6		7		8		9	
Matrix	N	L	N	L	N	F	N	F	N	F	N	F	N	F	N	F	N	F	N	F	N	F
Complete	180 (**74**)	719	94	723	44 (**22**)	89.49	44 (**22**)	72.26	44 (**22**)	61.25	44 (**22**)	53.45	40 (**22**)	47.53	48 (**22**)	42.87	48 (**22**)	39.08	48 (**22**)	35.94	48 (**22**)	33.28
m_noCh_noPat	40 (**20**)	718	24	722	44 (**11**)	88.99	22 (**11**)	71.99	22 (**11**)	61.1	22 (**11**)	53.39	24 (**11**)	47.49	24 (**11**)	42.84	48 (**22**)	39.05	24 (**11**)	35.91	24 (**11**)	33.25
m_noCh_noLep	8 (**6**)	718	4	722	4 (**2**)	88.99	2	71.99	2	61.1	2	53.39	2	47.49	2	42.84	4	39.05	2	35.91	2	33.25
m_noCh_noPat_noLep	2 (**2**)	718	1	722	2 (**1**)	88.99	1	71.99	1	61.1	1	53.39	1	47.49	1	42.84	2	39.05	1	35.91	1	33.25

	Value of *K*																			
	10		11		12		13		14		15		20		25		30		40		50	
Matrix	N	F	N	F	N	F	N	F	N	F	N	F	N	F	N	F	N	F	N	F	N	F
Complete	48 (**22**)	31	48 (**22**)	29.09	48 (**22**)	27.29	90 (**33**)	25.76	94 (**33**)	24.39	90 (**32**)	23.17	90 (**33**)	18.54	90 (**32**)	15.46	90 (**32**)	13.27	80 (**27**)	10.34	94 (**33**)	8.47
m_noCh_noPat	24 (**11**)	30.97	24 (**11**)	28.99	48 (**22**)	27.26	48 (**22**)	25.73	48 (**22**)	24.36	48 (**22**)	23.14	48 (**22**)	18.51	48 (**22**)	15.44	24 (**11**)	13.24	48 (**22**)	10.32	48 (**11**)	8.46
m_noCh_noLep	2	30.97	2	28.99	4	27.26	8 (**6**)	25.73	8 (**6**)	24.36	8 (**6**)	23.14	8 (**6**)	18.51	8 (**6**)	15.44	4 (**3**)	13.24	8 (**6**)	10.32	8 (**3**)	8.46
m_noCh_noPat_noLep	1	30.97	1	28.99	2	27.26	2	25.73	2	24.36	2	23.14	2	18.51	2	15.44	1	13.24	2	10.32	2 (**1**)	8.46

	Value of K									
	60		70		80		90		100	
Matrix	N	F	N	F	N	F	N	F	N	F
Complete	90 (**33**)	7.18	90 (**32**)	6.23	80 (**32**)	5.5	80 (**33**)	4.92	70 (**33**)	4.46
m_noCh_noPat	40 (**22**)	7.17	24 (**11**)	6.22	48 (**22**)	5.49	48 (**22**)	4.92	48 (**22**)	4.45
m_noCh_noLep	8 (**6**)	7.17	4 (**3**)	6.22	8 (**6**)	5.49	8 (**6**)	4.92	8 (**6**)	4.45
m_noCh_noPat_noLep	2	7.17	1	6.22	2	5.49	2	4.92	2	4.45

C. catia, n. sp., and *C. pachygnathoides*, n. sp., form a clade basal to a large group that includes all other species. Within this larger clade most of the relationships are unresolved except for two small clades. One of them, as in the previous analyses, includes all Caribbean Islands endemics except *C. bryantae*. The other clade comprises the species *C. atopica*, n. sp., *C. eberhardi*, n. sp., and *C. morona*, n. sp. A small clade composed by the species *C. waorani*, n. sp., and *C. leviorum*, n. sp. is basal to this large group of species.

The successive weighting analysis results in four trees of 722 steps (CI = 34, RI = 74) that are stable after the second iteration. The strict consensus of these MPTs is presented in figure 75 (L = 734 steps, CI = 33 and RI = 73). As in the analyses of the previous two matrices, the only difference with the equal weights parsimony results is the grouping of all Metinae sensu stricto genera in a monophyletic group basal to all other tetragnathids (fig. 75). Implied weighting analyses gave the same topologies as the analyses of the previous two matrices, with the only difference that the relationships within *Cyrtognatha* were better resolved.

M_NOCH_NOLEPPAT MATRIX. Removal of the four taxa with most missing entries results in a decrease of optimal trees. Two MPTs (L = 718 steps, CI = 34.4, RI = 74.5) are found under equal weights analysis (fig. 76). Figure 77 depicts its strict consensus cladogram (L = 719 steps, CI = 34.4, RI = 74.4). The main groups within Tetragnathidae and their relationships are the same as in the analysis of the other three matrices (see above). Five clades, in addition to "nephilids", can be defined: *Mollemeta*, Metinae *Meta* group, Metinae *Nanometa* group, Leucaugines, and Tetragnathinae. As in the previous analyses, the Metinae sensu stricto (Álvarez-Padilla, 2007) appear as three different clades. *Cyrtognatha* is monophyletic and is placed in the subfamily Tetragnathinae where its closest relative is *Tetragnatha*. *Mollemeta* is recognized as the most basal tetragnathid distal of "nephilids". The rest of the Metinae sensu stricto lineages also occupy basal position with respect to Leucaugines and Tetragnathinae. The main difference with analyses of the other three matrices is observed in the topology of the *Cyrtognatha* clade. Here, instead of a polytomy, the results show much better resolved relationships of the included species. *C. paradoxa* occupies a basal position with respect to all other *Cyrtognatha* species. Four clades with more than one member can be defined (fig. 77): the "*quichua* clade" includes *C. quichua*, *C. catia*, and *C. pachygnathoides*; the "*morona* clade" includes *C. morona*, *C. atopica*, and *C. eberhardi*; the "*orphana* clade" includes *C. orphana*, *C. nigrovittata*, *C. insolita*, and *C. petila*; and the "*bella* clade" includes *C. bella*, *C. bryantae*, *C. espanola*, *C. rucilla*, *C. simoni*, and *C. serrata*. The *morona*, *orphana*, and *bella* clades form a larger group in which the *morona* lineage occupies the most basal position. Although the strict consensus of the two MPTs resulting from this matrix improves the resolution of *Cyrtognatha*, the clades that receive support based on resampling methods are almost the same as in the analyses of the m_noCh_noLep matrix (see fig. 77). The group (*Glenognatha* + *Pachygnatha*) + *Tetragnatha* + *Cyrtognatha* receives very high support (more than 95) independently of the resampling method. The monophyly of each of these three genera is also very highly supported, with values ranging from 76 to 99. However, the clade *Tetragnatha* + *Cyrtognatha* does not receive support from these approximations. The only groups within *Cyrtognatha* that show higher support values are the *bella* clade (but without *C. bella*), the *quichua* clade (jackknife, standard bootstrap), and *C. atopica* + *C. eberhardi* (Poisson bootstrap and symmetric resampling). Only when Bremer support is used do most of the groups within *Cyrtognatha* obtain a support value of 1. Interestingly, the two nodes with higher Bremer support are the traditional Tetragnathinae (*Glenognatha* + *Pachygnatha* + *Tetragnatha* + *Cyrtognatha*) with Bremer support of 12 and *Cyrtognatha* with Bremer support of 13.

The successive weighting analysis of the matrix m_noCh_noLepPat finds a single tree (fig. 78; L = 722 steps, CI = 34, RI = 74). The topology of the *Cyrtognatha* clade is the same as in the results from the equal weights parsimony analysis, but here the relationships within the *bella* clade are better resolved. Under successive weighting there are three lineages of Metinae sensu stricto.

The *Nanometa* group is the most basal lineage in this clade, and the *Meta* + *Metellina* + *Dolichognatha* group is no longer monophyletic. Metinae sensu stricto is basal to all other tetragnathids except for the "nephilids".

Parsimony analyses under implied weighting criteria found very few trees, often only one (see table 2 for corresponding statistics). When $K = 1$ or 3 (fig. 79A, $K = 2$) the relationships within *Cyrtognatha* change and the clade *quichua* is no longer recognized as a monophyletic group. As in results with low values of K from the analyses of the other matrices, *Diphya* no longer belongs to Tetragnathinae but is placed in Metinae. Similarly, *Chrysometa* is not monophyletic and *Chrysometa acinosa* is recognized as the most basal Tetragnathinae. The rest of the *Chrysometa* species and *Allende* are placed as basal tetragnathids ($K = 1$) or as closest relatives of Tetragnathinae ($K = 2$–3). When $K = 1$ "nephilids" are included in Tetragnathidae and grouped with several Metinae genera (*Dolichognatha*, *Meta*, *Metellina*, and *Mollemeta*). Results stabilize when K is greater than 9, and there are basically two topologies. When K is between 9 and 20 (see fig. 79B for $K = 10$), the resolution for the Metinae sensu stricto is as with the successive weighting analysis (except for the interval $K = 9$–12). When K is in this range, the relationships within *Cyrtognatha* significantly change: *C paradoxa* is again the most basal member of *Cyrtognatha*, followed by a clade formed by *C. leviorum* and *C. waorani*. *C. bella* is not recognized as being closely related to the Caribbean Islands endemics, and instead it groups with the "*quichua* clade". When K is greater than 20 (see fig. 79C for $K = 25$), the results recover the same topology as in the equal weights analysis.

DISCUSSION

One of the main objectives of our cladistic analyses was to test the monophyly of the genus *Cyrtognatha* and to investigate its phylogenetic placement within Tetragnathidae. Our study also tests in a phylogenetic framework the proposed synonymy for the *Agriognatha* with *Cyrtognatha* and attempts to reconstruct the phylogenetic relationships within *Cyrtognatha*. The character matrix has representatives of 43% of the Tetragnathidae genera (all "Nephilidae" and Tetragnathinae genera are represented) and many other araneoids (six families represented), and therefore it allows us to make inferences about higher level relationships within Tetragnathidae, including the placement of *Nephila* and its close relatives.

Many of the implied weights analyses with low values of K result in "unconventional" topologies where most of the families and many of the genera were not monophyletic (see "Results from the Cladistic Analyses"). Low values of K weight homoplasious characters very strongly and its use is discouraged (Goloboff, 1993b, 1995). The topologies from these analyses were mentioned in the results section but are not discussed any further.

As a preferred hypothesis for the relationships for *Cyrtognatha*, we have chosen the results from equal weight parsimony analyses of the m_noCh_noPat_noLep matrix. These results are consistent with results from the other matrices analyzed but give much better resolution for the interspecific relationships of *Cyrtognatha*. When results from successive weighting or implied weighting analyses suggest different resolution, they are discussed where appropriate.

Araneoidea

Araneidae, the reduced piriform clade (Griswold et al., 1998), Tetragnathidae, and "Nephilidae" are monophyletic. In all analyses Araneidae is sister to all other Araneoidea. These results corroborate the basal placement of Araneidae as hypothesized by Coddington (1990), Hormiga et al. (1995), Griswold et al. (1998), Kuntner (2005, 2006), and Álvarez-Padilla (2007), but differ from the results of Schütt (2002). The interfamilial relationships within the reduced piriform clade taxa are out of the scope of this paper and are discussed elsewhere (Griswold et al., 1998; see also Lopardo and Hormiga, 2008). "Nephilids" are placed in Tetragnathidae, as in Hormiga et al. (1995), Griswold et al. (1998), and Álvarez-Padilla (2007). These results differ from the relationships proposed by Kuntner (2005, 2006, 2007), who hypoth-

esized that tetragnathids are more closely related to the reduced piriform clade than to "nephilids" (Kuntner's analyses used essentially the same character data for various taxonomic samples of species). Kuntner (2006) proposed raising to family rank ("Nephilidae") the group formed by the genera *Clitaetra* Simon, 1889, *Herennia* Thorell, 1877, *Nephilengys* L. Koch, 1872, and *Nephila* Leach, 1815. Kuntner (2006: 20) argued that based on his cladistic analyses "nephilines are not tetragnathids, and thus are proposed to be treated as a family", although none of his analyses offered an unambiguous hypothesis for the placement of nephilines within Araneoidea. In his preferred cladogram (Kuntner, 2006: fig. 27B) the family Tetragnathidae would be paraphyletic (with respect to the "Reduced piriform clade") if it were to include the nephilines (although his exclusion of *Phonognatha* from "nephilids" rendered Tetragnathidae paraphyletic!). It seems that by raising nephilines to family rank, Kuntner (2006) would circumvent the nomenclatorial problems derived from the uncertain phylogenetic placement of this lineage. Surprisingly, some of the most parsimonious cladograms resulting from the various analyses of Kuntner (2006: 24; 2005: 423; 2007: 99) suggest that the sister group of his "nephilids" is the Araneidae, that is, that nephilines are indeed an araneid lineage. Hypotheses about the araneid placement of nephilines go back to Simon's (1894) classification and were the conventional view until Levi (1986) and Levi and Eickstedt (1989) placed Nephilinae within Tetragnathidae. More recently, several authors have suggested again that *Nephila* and its relatives may belong within the Araneidae (e.g., Wunderlich, 1986, 2004; Pan et al., 2004) rather than within the Tetragnathidae. In previous phylogenetic analyses nephilines were hypothesized to be the most basal lineage of Tetragnathidae and to include the Australian genus *Phonognatha* (Hormiga et al., 1995; Griswold et al., 1998; Álvarez-Padilla, 2007). Our results corroborate the generic relationships within nephilines proposed by Hormiga et al. (1995) and Álvarez-Padilla (2007) and therefore differ from those of Kuntner (2005, 2006). This study as well as that of Álvarez-Padilla (2007) were not intended as a test of higher relationships of Araneoidea, but both have a much denser taxon sample of araneoids compared to Kuntner (2005, 2006). In light of these results we think that more studies are needed in order to resolve araneoid relationships (see also Griswold et al., 2005, and Lopardo and Hormiga, 2008), particularly the placement of *Nephila* and its relatives. It has been long recognized that nephilines have numerous unique characters, but we think that given the uncertainty about its phylogenetic placement, combined with the ongoing addition of comparative data relevant to this problem (e.g., Álvarez-Padilla, 2007; Álvarez-Padilla et al., 2007, in press) and the possibility that nephilines are indeed araneids, the change to family rank is at best premature. Justifying a change in family rank based on ambiguous phylogenetic results is hardly appealing, particularly when the available data cannot rule out the possibility of an araneid placement.

Tetragnathidae Including "Nephilidae"

In all analyses Tetragnathidae is monophyletic, but it receives very low Bremer support and none from the resampling methods. Three synapomorphies support the monophyly of this family: absence of median apophysis (char. 61[1]), conductor wrapping the embolus (char. 62[1]), and the flat epigynal plate (char. 90[4]). When the data are analyzed under successive weighting, the conductor path, starting from the margin of the tegulum and enclosing the embolus, provides an additional synapomorphy (char. 63[1]).

"Nephilidae"

"Nephilids" always appear as a monophyletic group (and include *Phonognatha* as the most basal lineage); however, this group does not receive support from any of the resampling methods and shows low Bremer support (it ranges from 2 to 4). Unambiguous synapomorphies supporting the monophyly of "nephilids" include: folded margin of the paracymbium (char. 54[2]); conductor covering all the embolus (char. 64[1]); threadlike (filiform) embolus (char. 73[1]); hub bite-out

absent (char. 96[0]); sticky spiral remaining in the finished web (char. 101[1]); sticky spiral located on oL4 (char. 103[2]); hub displaced upward (char. 158[1]); presence of secondary split radii (char. 160[1]); and presence of tertiary split radii (char. 161[1]). Under successive weighting character 64 (conductor covering all the embolus) becomes plesiomorphic and character 95[1] (hub against the substrate) provides an additional synapomorphy.

Metinae sensu stricto

Metinae sensu stricto, as defined by Álvarez-Padilla (2007), is polyphyletic. The uniformly weighted parsimony analysis support three separate lineages of Metinae: *Mollemeta*, the *Meta* group, and the *Nanometa* group. The *Mollemeta* lineage includes only the monotypic genus *Mollemeta*.

The *Meta* group includes *Meta*, *Dolichognatha*, *Metellina*, *Allende*, and *Chrysometa*, and its monophyly is supported by five synapomorphies: presence of metine embolic apophysis (char. 72[1]), female sternal tubercles III (char. 115[1]), elongated slit copulatory openings (char. 132[0]), copulatory ducts as short as broad and broad attachments to the body wall (char. 133[2]), and a short embolus (char. 154 [2]).

The *Nanometa* group includes *Nanometa* Simon, 1908, *Orsinome sarasini* Berland, 1924, and "Metinae from Australia", which all share two synapomorphies: the presence of several spines on the cymbial basal process (char. 44[4]) and the presence of a membranous sac that encloses the copulatory ducts (char. 87[1]).

None of these three lineages receives support from the resampling methods, and all of them have Bremer support of 1. Successive weighting and implied weighting analyses (under certain *K* values; see above) recover the Metinae sensu stricto group as described by Álvarez-Padilla (2007). However, this alternative topology does not receive high support.

In the results of the successive weighting, the monophyly of Metinae sensu stricto is supported by the following synapomorphies: presence of a cymbial median process (char. 46[1]), longer than wide and fingerlike paracymbium (char. 53[1]), conductor originating from the margin of the tegulum and following the tegular margin (char. 63[3]), conductor covering only part of the embolus (char. 64[2]), and female sternal tubercle I present (char. 113[1]). When this topology is found by implied weights the members of this group share the same synapomorphies except for the female sternal tubercle I. At least one of the synapomorphies supporting Metinae sensu stricto as a monophyletic group, the cymbial median process, is not found in any other Tetragnathids but is present in some out-groups (e.g., *Pimoa* Chamberlin and Ivie, 1943).

When recovered as a monophyletic group, Metinae sensu stricto keeps the three already defined lineages (*Mollemeta*, *Meta* group, and *Nanometa* group). It is clear that more studies are needed to test the monophyly and relationships of these metine lineages, and under such circumstances we prefer not to name subfamilies and other higher taxa. We should mention that Forster and Forster placed the genus *Nanometa* and the species *Orsinome lagenifera* (Urquhart, 1888) in a separate family, Nanometidae. Recognizing this Austral lineage as a family, however, would render Tetragnathidae paraphyletic.

The two species of *Orsinome* included in the analysis were never recovered as a monophyletic group. This was already suggested in the analysis of Álvarez-Padilla (2007). *Orsinome* as currently circumscribed is not monophyletic and the genus requires a modern taxonomic revision.

Leucaugines

Leucaugines sensu Álvarez-Padilla (2007) is always recovered as a monophyletic group independent of the character weighting treatment and the sample of taxa included in the analyses. This clade includes the genera *Azilia*, *Orsinome* Thorell, 1890, *Tylorida* Simon, 1894, *Leucauge*, *Metabus* O.P.-Cambridge, 1899, *Mesida* Kulczynski, 1911, and *Opadometa* Archer, 1951. The clade *Orsinome*, *Tylorida*, *Leucauge*, *Metabus*, and *Mesida* plus *Opadometa* without *Azilia* always receives support higher than 50 from the resampling approximations and shows one of the highest Bremer support values (5) on the tree.

Leucaugines including *Azilia* is supported by eight synapomorphies: ectally displaced subtegulum (char. 55[1]), highly coiled sperm reservoir (char. 59[1]), reservoir with a switchback (char. 60[1]), ventrally enlarged tegulum (char. 57[1]), and nonsclerotized spermathecae (char. 85[1]) (these synapomorphies were already discussed by Álvarez-Padilla, 2007). The presence of a sternal tubercle III in the females (char. 115[1]); the transparent cymbial ectal margin (char. 144[1]), and the absence of fovea pits (char. 194[0]) are reported for the first time herein as additional synapomorphies of Leucaugines.

Tetragnathinae

Tetragnathinae includes the genera *Diphya*, *Pachygnatha*, *Glenognatha*, *Tetragnatha*, and *Cyrtognatha*. *Diphya* is sister to a clade that includes all other Tetragnathinae genera. *Glenognatha* + *Pachygnatha* is sister to the clade *Tetragnatha* + *Cyrtognatha* in all analytical treatments, but only the first clade receives significant support. The group (*Pachygnatha* + *Glenognatha*) + (*Cyrtognatha* + *Tetragnatha*) is recovered in all analyses and always receives very high support (more than 95 in all resampling approximations; its Bremer support, 12, is the second highest). In previous analyses *Diphya* was not recognized as a close relative of the other genera in Tetragnathinae (Schütt, 2002), or when placed in Tetragnathinae this placement was regarded as questionable since this genus does not show some of the most characteristic features of Tetragnathinae (Álvarez-Padilla, 2007; Dimitrov et al., 2007). Five synapomorphies support the Tetragnathinae (including *Diphya* as the basal lineage): distally swollen paracymbium (char. 51[1]), presence of anterior paracymbium apophysis (char. 54[1]), paired white spots around the spinnerets in the female (char. 126[1]), male chelicerae larger than in the female (char. 139[1]), and the presence of a tubercle on the male paturon (char. 147[1]). Seventeen synapomorphies (seven of them nonhomoplasious) support the clade that includes all Tetragnathinae except *Diphya*: cheliceral curvature of the male more than twice the cheliceral width (char. 15[1]), femur with dorsal trichobothria (char. 27[0]), constricted cymbium (char. 38[1]), absence of the cymbial basal process (char. 41[0]), articulated paracymbium (char. 50[3]), enlarged sperm reservoir (char. 58[1]), conductor originating from the center of the tegulum and coiling with the embolus (char. 63[2]), absence of epigynum (char. 79[1]), absence of fertilization ducts (char. 80[1]), copulatory openings immersed in a sac (char. 81[2]), epigynum without epigynal plate (char. 90[0]), female PME less than one diameter apart (char. 108[0]), absence of female sternal tubercle I (char. 113[0]), copulatory opening as a transverse groove (char. 132[2]), long cymbium (char. 143[1]), moderately divergent chelicerae (char. 171[1]), and epigynum with a saclike chamber connecting to the uterus externus (char. 188[1]). Several of these synapomorphies were previously described by Álvarez-Padilla (2007).

Cyrtognatha

A clade that includes all the species in the genera *Agriognatha* and *Cyrtognatha* is recovered by all analyses. Discussion of the relationships and synapomorphies for *Cyrtognatha* are based on the results form the analyses of the m_noCh_noPat_noLep matrix (which does not include *Chrysometa levii*, *Ch. maitae*, *Cyrtognatha lepida*, and *C. pathetica*), as they are based on a matrix with significantly reduced missing data, which results in more resolved topologies (figs. 76–78). *Cyrtognatha* monophyly is very well supported, showing the highest Bremer support (13) and very high values for the resampling indices (bootstrap, 99; Poisson bootstrap, 99; jackknife, 99; and symmetric resampling, 99; similar values are obtained with the other matrices). Thirteen unambiguous synapomorphies support the monophyly of *Cyrtognatha*, six of which are free of homoplasy: characteristic macrosetae on the PLS (char. 169[1], an autapomorphy of the genus), apical embolic membrane (char. 176[1]), conductor with a basal apophysis (char. 181[1]), triangular apical apophysis of the conductor (char. 183[1]), absence of spermathecae (char. 186[1]), and posterior

sac of the vulva modified as a sperm storage organ (char. 190[1]). Additional synapomorphies of *Cyrtognatha* are: the rugose anterior cheliceral surface in males (char. 20[1]), branched trichobothria on femur IV (char. 29[2]), IV femoral trichobothria extending over more than a third of the femur (char. 30[1]), paracymbium without apophyses (char. 54[0]), conductor covering only partially the embolus (char. 64[2]), female abdomen with anterior humps (char. 123[1]), and smooth male paturon (char. 147[0]).

Several clades can be defined within *Cyrtognatha*, but most of them do not receive high clade support values. Furthermore, most of the species are known from just one of the sexes, and the number of species combined with their geographic distribution suggests that many species await discovery. Updating the matrix with data for the missing sexes and/or newly discovered species might lead to changes of the relationships described herein. Nevertheless, our discussion is based on the best possible taxonomic representation and includes all the evidence that we could collect. Based on our results, we have recognized and informally named four species groups within *Cyrtognatha* (fig. 77): the *quichua*, *morona*, *orphana*, and *bella* groups.

The *quichua* clade includes *C. quichua*, *C. catia*, and *C. pachygnathoides*. These species share the following synapomorphies: conductor basal apophyses with reduced membrane apically (char. 182[0]), MEA with extensive prolateral fold (char. 185[1]), males with a well-developed distal tubercle of the abdomen (char. 191[1]), distal tubercle of the abdomen vertical (char. 192[1]), tip of the basal apophysis of the conductor without outgrowths (char. 193[0]).

The *morona* clade includes *C. morona*, *C. eberhardi*, and *C. atopica*. Two synapomorphies support this group: cheliceral dorsal tooth outlying the fangal joint (char. 173[1]) and presence of basal apophysis of the embolus (char. 180 [1]). In the results from the analyses of the matrix m_noCh_noLep, *C. waorani* and *C. leviorum* are grouped together, but neither of these alternative topologies receives significant support.

The *orphana* clade includes *C. orphana*, *C. nigrovittata*, *C. insolita*, and *C. petila*. A single unambiguous synapomorphy supports this group, namely the presence of the embolus serrated membrane (char. 184[1]).

The *bella* clade includes the species from the West Indies (*C. bryantae*, *C. simoni*, *C. espanola*, *C. rucilla*, and *C. serrata*) and *C. bella*. One synapomorphy supports the monophyly of the *C. bella* clade: the absence of the metine embolic apophysis (char. 72[0]). The clade formed from the West Indies species is supported by two synapomorphies: small conductor (char. 152[0]) and basal apophysis of the conductor without apical membrane (char. 182[0]).

If *Agriognatha* were to be kept as a genus separate from *Cyrtognatha*, its composition would correspond to the *bella* clade (which includes its type species, *Agriognatha bella*). Such a proposal would be untenable because the assemblage that includes all remaining species (including the type species of *Cyrtognatha*, *C. nigrovittata*) is a paraphyletic group.

The limitations about the taxonomic knowledge of *Cyrtognatha*, particularly the likely existence of many undiscovered species, hinder an in-depth study of the biogeography of this genus. The present analyses suggest at least one dispersal event from North to South America and two from South to North America (fig. 80). To explain the species diversity within these continents, several vicariance events can be postulated, but our knowledge of the species distributions is very limited, so any inference about it would be highly speculative. The same is true for the Caribbean endemics. With the present data it is practically impossible to hypothesize if they are the result of a vicariance or dispersal events or a combination of both. Three models attempting to explain the peculiar biota of the Caribbean Islands were proposed during the last century. The first ones are the models suggesting a vicariant origin of the Caribbean fauna (Crother and Guyer, 1996; Rosen, 1975, 1985; Liebherr, 1988; Page and Lydeard, 1994; Guyer and Crother, 1996). The land bridge model (Scharff, 1912; Barbour, 1916; Schuchert, 1935; MacPhee and Iturralde, 1994, 1995; Iturralde and MacPhee 1999; Woods, 2001) was proposed as a modification to the vicariance that does not imply dispersal events. Finally, with the

increasing availability of molecular data and based on molecular clock estimates, dispersal was used to explain the origin of several groups of terrestrial animals (Hedges et al., 1992, 1994; Hedges, 1996a, 1996b, 2001). There is an active discussion in the scientific community on which of these models better explains the observations. The most recent overview on West Indies biogeography is that of Woods (2001). Our data on the biogeographic pattern are not conclusive in this sense, and the observed distribution could fit any of these models. However, it is interesting that the closely related genus *Tetragnatha* is known to disperse easily and that species of this genus have successfully colonized even the most remote oceanic archipelagos (Gillespie et al., 1994; Gillespie 2002).

Independently of the underlying colonization and speciation mechanisms, several general conclusions can be drawn about the phylogeographic relationships of the *Cyrtognatha* species.

1. The Mexican species *C. paradoxa* is always recovered as the most basal *Cyrtognatha*, and when geographic distribution is optimized, both under ACCTRAN and DELTRAN, the genus appears to have a Mexican origin.

2. The *bella* + *orphana* clade is of Central American origin. Although the locality where *C. orphana* was collected (São Paulo olov., Cuv-Cucho as written on the label) is in the same state as the type locality of *C. eberhardi* (São Paulo, Fazenda Intervales), these two species are not closely related and *C. orphana* is closer to some Central American species of the genus and to *C. nigrovittata* (from Peru).

3. All endemic species found on the Caribbean Islands share a common ancestor of Central American origin.

NATURAL HISTORY

Prior to our study there were almost no data available on the natural history of *Cyrtognatha* species. The only aspect of their life known with certainty was their preference for tropical cloud and lowland rain forests. According to our observations and to the locality data from the museum specimens, *Cyrtognatha* species are found either in lowland rain tropical forests or in cloud tropical forests. During the last few years we have been able to document the webs and habitats of a number of *Cyrtognatha* species.

Cyrtognatha rucilla builds its webs in humid cloud forests found at high elevation areas of Hispaniola. The web (fig. 2A–E) is inclined at different levels but is always less than 45°. It has an open hub and relatively few radii but numerous sticky spiral turns. The spider stays in the center of the web with extended legs I and II. Legs I, II, and IV are touching six different radii, while legs III are touching one of the spirals of the hub (fig. 2C). The web frame is rectangular with few attachment sites. There is no retreat; however, if the spider is disturbed it runs out of the web, leaving a drag line, which in some photos might be mistakenly interpreted as a "telegraph line" leading to a retreat (fig. 2B). However, unlike real telegraph lines leading to retreats off the web (e.g., in *Azilia*), this drag line touches sever spirals.

Cyrtognatha espanola lives in the same habitats as *C. rucilla*. The webs of these two species are very similar, but the web of *C. espanola* is slightly smaller and with fewer spirals that look more irregular (fig. 2F). Some webs of *C. espanola* were almost vertical, but due to the small sample size (two webs were photographed) it is difficult to decide whether it is a "typical" type or if both inclined and vertical webs are built indistinguishably. When this species was coded in the matrix a conservative decision to code the web angle as "?" was adopted. Unfortunately, we could not photograph specimens of this species in its web. We studied these two species in a cloud forest under high anthropic pressure with clear signs of past disturbances.

Cyrtognatha quichua (fig. 1A–C) spins its webs in the cloud forests of Ecuador. The web is practically horizontal (figs. 1D, 3A) with open hub and few radii, as in the other *Cyrtognatha* species. The number of spiral turns is relatively low compared to other *Cyrtognatha* species that we have observed, and there are again some lines that look like drag lines (fig. 3A).

Cyrtognatha petila is the *Cyrtognatha* species with the most peculiar habitus and at first glance it may look very similar to

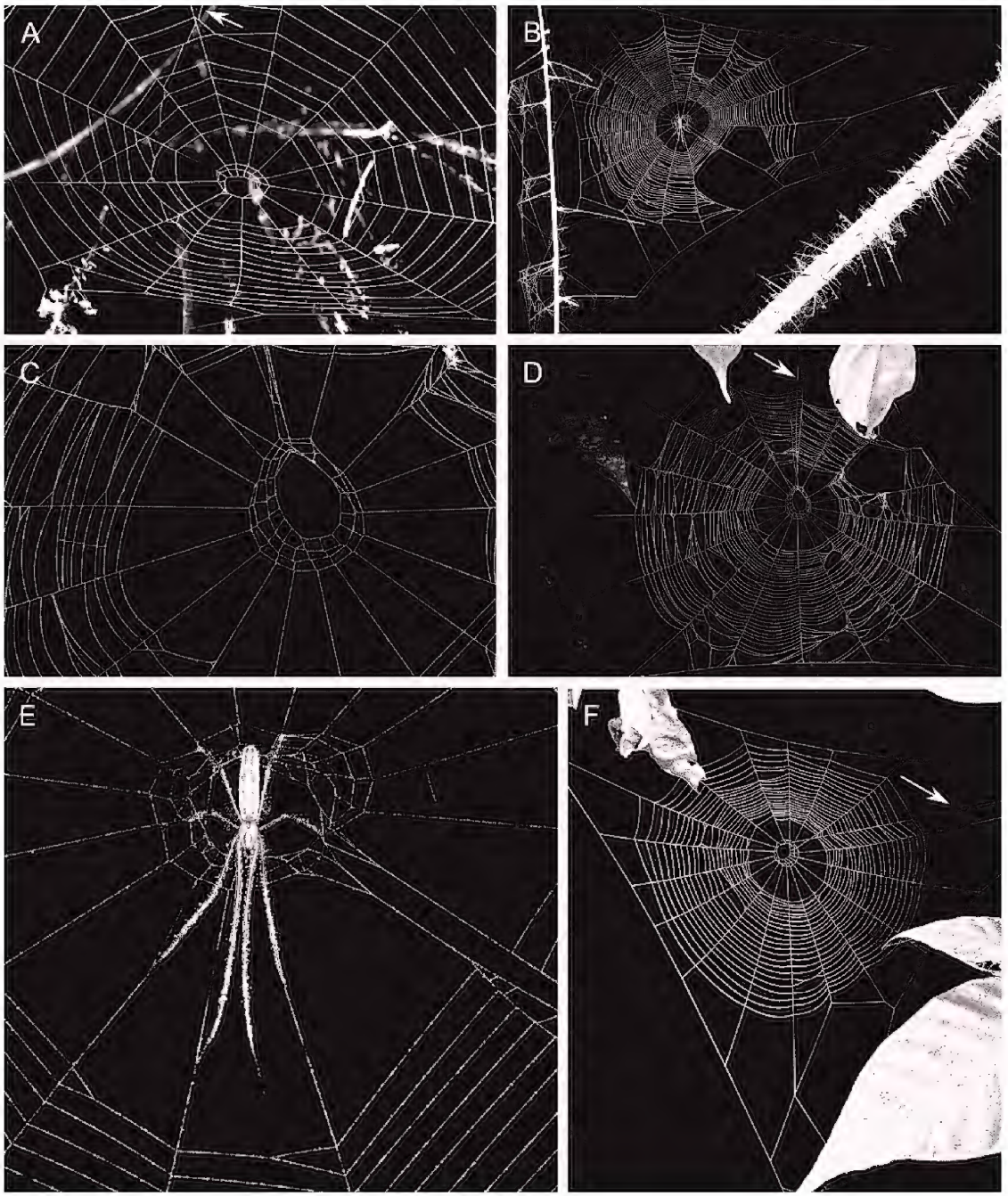

Fig. 3. Web of *Cyrtognatha quichua* (**A**) (from Ecuador, Sierra Azul). Webs and habitus of *Cyrtognatha petila* (**B–F**) (from, Mexico, Chiapas, Ocosingo, Sierra de la Cojolita, Arroyo Nayte). Arrows point to drag lines going out of the web; photos in 3B–F by Fernando Álvarez-Padilla.

Tetragnatha (fig. 3B, C). This species lives in lowland rain tropical forests of southeast Mexico. The webs of *C. petila* (figs. 3B–F, 4A) are very similar to those of the other *Cyrtognatha* species, but the web frame is almost triangular (fig. 3B, D, F) and the webs are less inclined. The spider awaits its prey in the center of the web with extended I

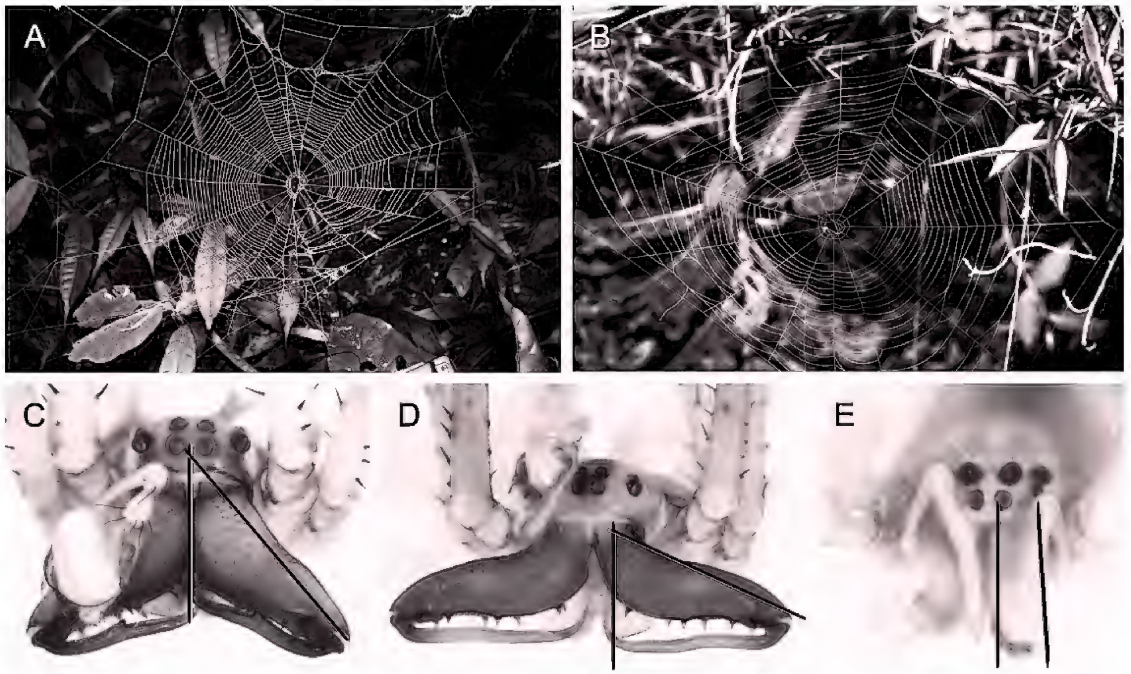

Fig. 4. Web of *Cyrtognatha petila* (**A**) (from Mexico, Chiapas, Ocosingo, Sierra de la Cojolita, Arroyo Nayte); photos by Fernando Álvarez-Padilla. Web of *Cyrtognatha catia* (**B**) (from Colombia, Valle del Cauca; maximum vertical web diameter 31.5 cm)—a drag line leading toward the vegetation near the web can be observed. Variation of the chelicerae divergence in *Cyrtognatha*. Moderately divergent chelicerae (**C**). Widely divergent chelicerae (**D**). Chelicerae without divergence (**E**).

and II pair of legs (F. Álvarez-Padilla, personal commun.). The diameters of the measured webs of *C. petila* were 26 cm, two of 18 cm, and 16 cm. In the photographed webs in which the spider was not at the hub, the drag lines were clearly observed (fig. 3D, F). Despite its similarity to the somatic morphology of many *Tetragnatha* species, one of the important diagnostic characters that separate these two genera, the feathered trichobothria of the femur IV, is clearly visible (fig. 3E).

Cyrtognatha catia is another species inhabiting tropical cloud forests in Colombia. It builds an almost horizontal web with few attachment sites and few radii and spirals (fig. 4B).

DISTRIBUTION

Cyrtognatha has a broad range of distribution, spanning over a large part of South America, Central America, and the southern parts of North America (fig. 5). The southernmost species are found in Brazil and the northernmost species in southern Mexico. Despite this wide distribution, most of the species are known from single localities and often just from a very few museum specimens. Several species are known from the Caribbean Islands of Cuba (one species), Hispaniola (two species), Jamaica (one species), and Saint Vincent (one species).

KEY TO THE SPECIES OF *CYRTOGNATHA* (MALES)

1. Caudal tubercle of the abdomen well developed (fig. 1A–C) 2
– Caudal tubercle very small or absent. . . . 7
2. Metine embolic apophysis distally finishing in a long (nearly as long as the distal embolus) lamina (fig. 9A–C) 3
– Metine embolic apophysis differently shaped 4
3. One of the three distal membranous processes of the basal apophysis of the conductor with

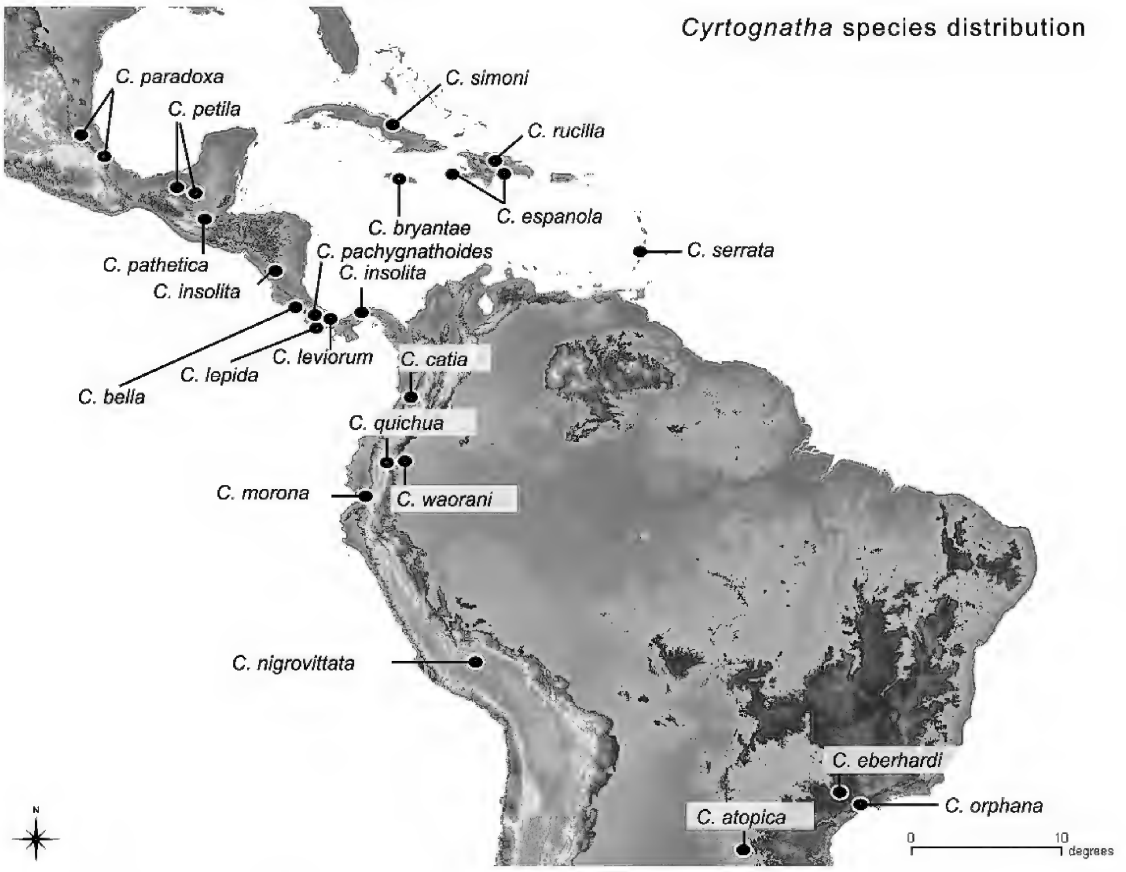

Fig. 5. Known distribution of the *Cyrtognatha* species. Due to scale limitations, when localities are very close to each other only one dot is used to represent them.

a well-chitinized sharpened outgrowth (fig. 10A, C); tip of the paracymbium widened and elongated (fig. 10B) . . . . . *C. eberhardi*, n. sp.

– Basal apophysis of the conductor with three membranous processes without sharpened outgrowth (fig. 9C); tip of the paracymbium rounded (fig. 9B). . . . . *C. atopica*, n. sp.

4. Embolus ventrally with a big metine embolic apophysis (fig. 62A); metine embolic apophysis nearly straight and without distinguishable longitudinal fold in prolateral view; abdomen cylindrical with long caudal tubercle oriented longitudinally (fig. 63A–C) . . . . . *C. nigrovittata*

– Metine embolic apophysis with a well-developed membrane between it and the rest of the embolus, which has numerous folds; metine embolic apophysis with a well-developed longitudinal fold prolaterally (fig. 25A) . . 5

5. Embolus widened subapically and with a semicircular subterminal outgrowth (fig. 25A–C); metine embolic apophysis with a well-developed longitudinal fold prolaterally, which runs through the whole length of the apophysis (fig. 25A) . . . *C. pachygnathoides*

– Distal part of the embolus (beyond the base of metine embolic apophysis) not widened 6

6. Embolus with a membranous lamina reaching its tip (fig. 11A); metine embolic apophysis prolateral fold does not reach the base of metine embolic apophysis (fig. 11C); embolus tip in prolateral view not bended ventrally . . . . . *C. quichua*, n. sp.

– Membranous lamina on the embolus not reaching embolic tip (fig. 8A, B); metine embolic apophysis with prolateral fold starting from its base. 8C); embolus tip in prolateral view bent ventrally . . . . . *C. catia*, n. sp.

7. Chelicerae widely divergent (fig. 4B) 8

– Chelicerae moderately divergent (fig. 4A) . . 16

8. Tip of the embolus bent prolaterally (fig. 22A) . . . . . *C. orphana*, n. sp.

– Tip of the embolus differently shaped . . . 9
9. Distal part of conductor basal apophysis wider than its base in prolateral view (fig. 16C) 10
– Distal part of conductor basal apophysis narrower than its base in prolateral view (fig. 41C) 12
10. Embolus with a conspicuous distal apophysis (DEA) (fig. 16A,B) . . . . . *C. morona*, n. sp.
– Embolus without distal apophysis. 11
11. Embolus with enlarged section (fig. 15A, B); basal apophysis of the conductor ends distally with a bifurcated flattened apophysis with short sharpened outgrowths (fig. 15C); embolus with well-developed metine embolic apophysis (fig. 15A–C) . . *C. waorani*, n. sp.
– Embolus not enlarged (fig. 15A); basal apophysis bifurcated distally but rounded (fig. 15C); embolus without metine embolic apophysis and with a terminal membrane and ventral folds (fig. 15A–C). . . . . *C. paradoxa*, n. sp.
12. Dorsal tooth of the chelicerae bifurcated (fig. 38B–E); continental Central America 13
– Dorsal tooth of the chelicerae not bifurcated; Greater Antilles 14
13. Metine embolic apophysis very well developed (fig. 37A–C; embolus widened and with an extensive serrated membrane between its distal part and the metine embolic apophysis (figs. 37A, C, 39A, B, 39I) . . . . . *C. insolita*
– Embolus without metine embolic apophysis (fig. 58A–C); embolus without serrated membrane (fig. 58C). . . . . *C. bella*
14. Apical apophysis of the conductor with two almost equally developed processes (fig. 52B); embolus without metine embolic apophysis and with a short membrane ventrally from its distal edge (fig. 52A, C); Jamaica . . . . . *C. bryantae*
– Apical apophysis of the conductor with one process much bigger than the other (fig. 41A); embolus without membrane and metine embolic apophysis 15
15. Tip of the embolus curved prolaterally (fig. 31A); embolus as in fig. 31A–C; Hispaniola . . . . . *C. espanola*
– Tip of the embolus pointing retrolaterally (fig. 47A, B); embolus as in fig. 47A–C; Cuba . . . . . *C. simoni*
16. Embolus with a well-developed triangular metine embolic apophysis apophysis ventrally (fig. 18A); embolus very wide subterminally and with a serrated membrane (fig. 18A–C) . . . . . *C. petila*, n. sp.
– Embolus with a very small or without metine embolic apophysis; embolus without serrated membrane 17
17. Distal part of the basal apophysis of the conductor wider than its base (fig. 17A, C); large portion of embolus with a distal membranous ridge; metine embolic apophysis very small (fig. 17A, B) . . *C. leviorum*, n. sp.
– Distal part of the basal apophysis of the conductor narrower than its base (fig. 60C); embolus without metine embolic apophysis, and if membranous ridge is present it does not reach the embolic tip (fig. 60C). 18
18. Apical apophysis of the conductor with two with two processes of similar size (fig. 60B); embolus with a membrane ventrally near the narrower distal edge of the embolus (fig. 60A–C); St. Vincent Island. . . . . *C. serrata*
– Apical apophysis of conductor with one distal process several times larger than the other (fig. 41A); embolus without membrane (fig. 41A–C); Hispaniola . . . . . *C. rucilla*

KEY TO THE SPECIES OF *CYRTOGNATHA* (FEMALES)

1. Caudal tubercle of the abdomen well developed (higher than one-third of the height of the caudal fraction of the abdomen) (fig. 30D) 2
– Caudal tubercle of the abdomen very small or absent (fig. 46F) 6
2. Internal female genitalia with two membranous sacs (fig. 31E) 3
– Internal female genitalia with one membranous sacs (fig. 37B) 4
3. Membranous chamber of the uterus externus larger or very similar in size to the median sac (fig. 25D–E); median sac proximally elongated with nearly cylindrical shape . . . . . *C. pachygnathoides*
– Membranous chamber of the uterus externus smaller than the median sac (fig. 31D–E); median sac rounded . . . . . *C. espanola*
4. Membranous chamber connecting the uterus externus and posterior sacs conspicuously widened and with a chitinized section that has a triangular shape in dorsal view (figs. 20D, E, 21E) . . . . *C. paradoxa*, n. sp.
– Membranous chamber connecting the uterus externus and the posterior sac not widened and without chitinized section 5
5. Membranous chamber connecting the uterus externus and the posterior sac almost straight (fig. 11E) . . . . . *C. quichua*, n. sp.
– Membranous chamber connecting the uterus externus and the posterior sac with a pronounced U curvature (fig. 52D). . *C. bryantae*
6. Internal female genitalia with one membranous sacs (fig. 37B) 7

– Internal female genitalia with two membranous sacs (fig. 31E) 11
7. Membranous chamber connecting uterus externus and posterior sac not widened . . 8
– Membranous chamber connecting uterus externus and posterior sac widened 9
8. Membranous chamber connecting uterus externus and posterior sac with a pronounced U curvature (fig. 22D) . . . *C. orphana*, n. sp.
– Membranous chamber connecting uterus externus and posterior sac almost straight (fig. 37D) . . . . . *C. insolita*
9. Membranous fold of abdominal cuticle forming the secondary genital opening about twice as wide than the width of the posterior sac (fig. 24A, B) 10
– Membranous fold of abdominal cuticle forming the secondary genital opening might be wider than the width of the posterior sac, but it does not exceed its width by more than 1.5 times (fig. 18D, E) . . . . . *C. petila*, n. sp.
10. Copulatory ducts clearly widened distally (fig. 59B) . . . . . *C. lepida*
– Copulatory ducts cylindrical (fig. 24B) and not widened or just slightly widened distally . . . . . *C. pathetica*, n. sp.
11. Posterior sac larger than the median sac (fig. 48B, D) . . . . . *C. simoni*
– Posterior and median sacs of similar size 12
12. Membranous fold of abdominal cuticle forming the secondary genital opening about twice as wide than the width of the posterior sac (fig. 60E); St. Vincent . . . . . *C. serrata*
– Width of the membranous fold of abdominal cuticle forming the secondary genital opening smaller than the width of the posterior sac (fig. 41G); Hispaniola . . . . . *C. rucilla*

TAXONOMY

Family Tetragnathidae Menge, 1866
Genus *Cyrtognatha*, Keyserling, 1881

Type species by original designation: *Cyrtognatha nigrovittata*, Keyserling, 1881.

Agriognatha, O. P.-Cambridge, 1896, new synonymy.

DIAGNOSIS: *Cyrtognatha* can be easily distinguished from all other tetragnathids by the presence of a straight line of long and robust macrosetae with enlarged bases on the retrolateral surface of the posterior lateral spinnerets (fig. 28A, G, J). Such macrosetae are unique to this genus and are present in males, females, and juveniles. These macrosetae are relatively large and can be easily observed using a stereomicroscope, even at relatively low magnifications, which allows the correct genus determination of immature specimens. The shape of the female internal genitalia is also diagnostic for *Cyrtognatha* (fig. 7) (see also Dimitrov et al., 2007). In *Cyrtognatha* the spermathecae are reduced and the sperm storage function is taken by an unpaired membranous structure (the posterior sac). The presence of this structure seems to be unique and therefore diagnostic for this genus. *Cyrtognatha* species can also be distinguished from other tetragnathids by the shape of the male chelicerae, which are not projected but are wider distally and conspicuously divergent in the distal two-thirds (e.g., figs. 1A–C, 8E–G).

The enlarged and highly modified embolus is also diagnostic. While in most tetragnathids and all Tetragnathinae the embolus is a thin cylindrical tube, in *Cyrtognatha* the embolus is widened, often as wide as half of the tegulum diameter (e.g., *C. insolita* and *C. morona*, figs. 37A–C and 16A–C, respectively). Within Tetragnathinae, males of *Cyrtognatha* further differ from *Pachygnatha* and *Tetragnatha* by having the paracymbium attached to the base of the cymbium (in *Pachygnatha* and *Tetragnatha* the paracymbium is a separate sclerite connected to the cymbium by means of a membrane). *Cyrtognatha* can be also easily distinguished from *Pachygnatha* by the shape of the sternum (which does not surround the coxae; figs. 8G, 48A), and from *Tetragnatha* by the shape of abdomen, which in *Cyrtognatha* is less elongated and more oval in shape, and often with well-developed dorsal tubercles. Also, the chelicerae are not projected, and the conductor is more complex. An additional diagnostic character separating *Cyrtognatha* from *Tetragnatha* (and other closely related genera) is the presence in the former genus of feathered trichobothria on the femur of the fourth leg (figs. 29F, 36B, 54I). Such trichobothria are widespread among leucaugine genera, but in *Cyrtognatha* feathered and nonfeathered trichobothria are alternated. The first four or five trichobothria near the base of the femur have short ramifications (feathered trichobothria) (fig. 29F). They are

followed by one trichobothrium, which is about twice as short and does not have such ramifications (smooth trichobothria). This nonfeathered trichobothrium is followed again by a feathered one, and this pattern is repeated (fig. 12H). Finally, *Cyrtognatha* also differs from other Tetragnathinae by its more complex conductor, which carries a very well-developed basal apophysis (fig. 6C) and an apical apophysis (fig. 6C–E).

DESCRIPTION: Small to medium size tetragnathid spiders; total body length 3.18–7.80 in males and 4.30–10.73 in females. Males slightly smaller than females. Carapace longer than wide, 1.47–3.10 long in males and from 1.75 to 3.90 long in females; light brown-yellowish to dark brown with a well-distinguished fovea. Sternum slightly longer than wide and prolonged between coxae IV. ALE on short lateral elevations and close to the PLE; AME and PME placed on the edges of an imaginary rectangle. AME on an elevation, often slightly higher in males. PME and AME slightly larger than the other eyes. Lateral eyes with nearly the same diameter. Clypeus height from one to twice the AME diameter in males. In females the clypeus is lower and its height ranges from 0.1 to 1.3 times the AME diameter. Labium trapezoidal, wider distally, dark in color, and almost as high as its maximum width. Endites elongated, divergent, and distally widened (figs. 29B, 35A, 38H). Chelicerae large and massive, sexually dimorphic, usually darker than the rest of the cephalothorax. Male chelicerae conspicuously divergent and not projected (e.g., figs. 1A–C, 38A–C; see also O.P.-Cambridge, 1896). The projected chelicerae relative to the cephalothorax is most likely a result of the dehydrating effect of alcohol and the resulting muscle contraction. The lack of observation in vivo, most likely, is the reason for describing the chelicerae of this genus as projected in the original description. Chelicerae distally wider and with a small cheliceral boss. Cheliceral fangs long, slightly curved, and with short retrolateral outgrowth (fig. 42B, D, E), which in some species can be smaller or absent (fig. 38B, F). Chelicerae distally with heavily sclerotized dorsal tooth close to the fang articulation (figs. 38E, 42E, H, 48H). In some species the dorsal tooth is reduced in size and it is similar to the distal teeth (e.g., *C. pachygnathoides*, fig. 26B). Distal margins of the chelicerae with three anterior and four posterior teeth. The number of cheliceral teeth does not usually vary between and within species and between males and females, but one specimen with five posterior teeth on one of the chelicerae was found in a male of *C. petila* (in this case the specimen had four teeth on the other chelicerae, and specimens from the same species had four teeth on both chelicerae as well). Female chelicerae are less divergent, without the distal tooth, cylindrical, and not widened distally; the teeth on the distal margin are closer to each other. Legs carry numerous setae and strong dark colored spines; legs slightly longer in males than in females (figs. 11H, 21A, B). Leg I is the longest and leg III is the shortest. Tarsus and distal part of the metatarsus without spines. Femur I length varies from 3.67 to 6.82 in males and from 1.86 to 5.88 in females. Abdomen elongated, longer than wide, of very variable coloration, from brownish with reflecting guanine spots and green and reddish tones to yellowish, almost totally covered with guanine causing silvery reflecting appearance (figs. 11H, 26A, C, D). Live specimens that were observed during this study presented distinct and more vivid coloration compared to specimens preserved in alcohol. Some of the pigments (especially the one responsible for the green coloration) are quickly degraded in alcohol and fade fast to brown-yellowish. Brownish pigments appear to be more resistant but also fade gradually with time. Abdomen dorsally with two lateral tubercles on its proximal edge (in some species these tubercles are reduced and the abdomen is just swollen proximally). Some species have a third distal caudal tubercle (e.g., figs. 30D, 63A–C). Height of distal tubercle varies greatly between and within species and in some cases it may be as high as or higher than the abdomen. Several species that lack a caudal tubercle have a distinctive abdominal tubercle placed dorsally, close to the half length of the abdomen (e.g., *C. espanola*, fig. 36F). Ventrally the guanine spots are fewer and smaller; in many species a darker band is present starting just after the genital opening.

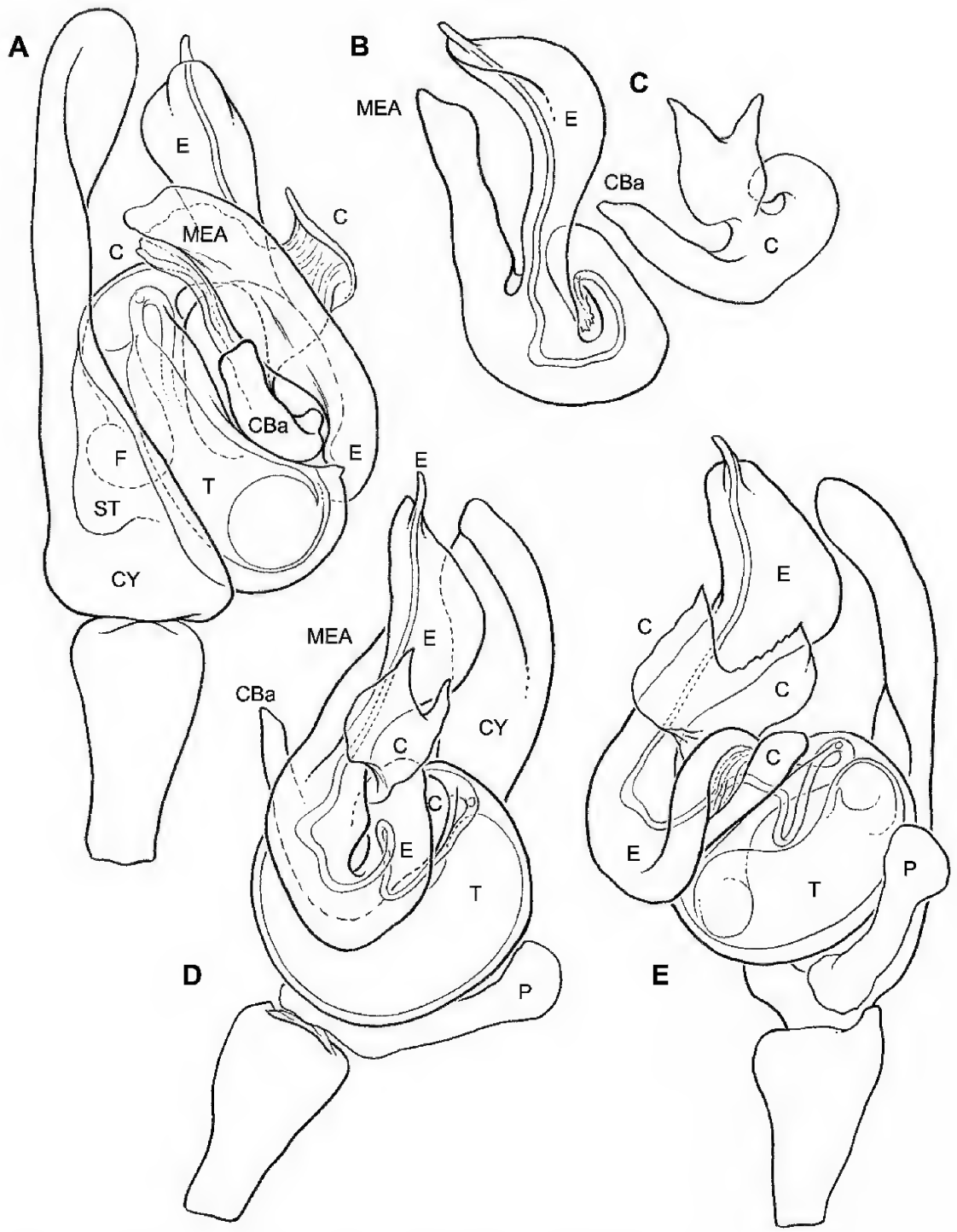

Fig. 6. Schematic drawings of the male palp of *Cyrtognatha* (the species depicted is *C. pachygnathoides*). Palp prolateral (**A**), embolus (**B**), conductor (**C**), palp ventral (**D**), palp retrolateral (**E**).

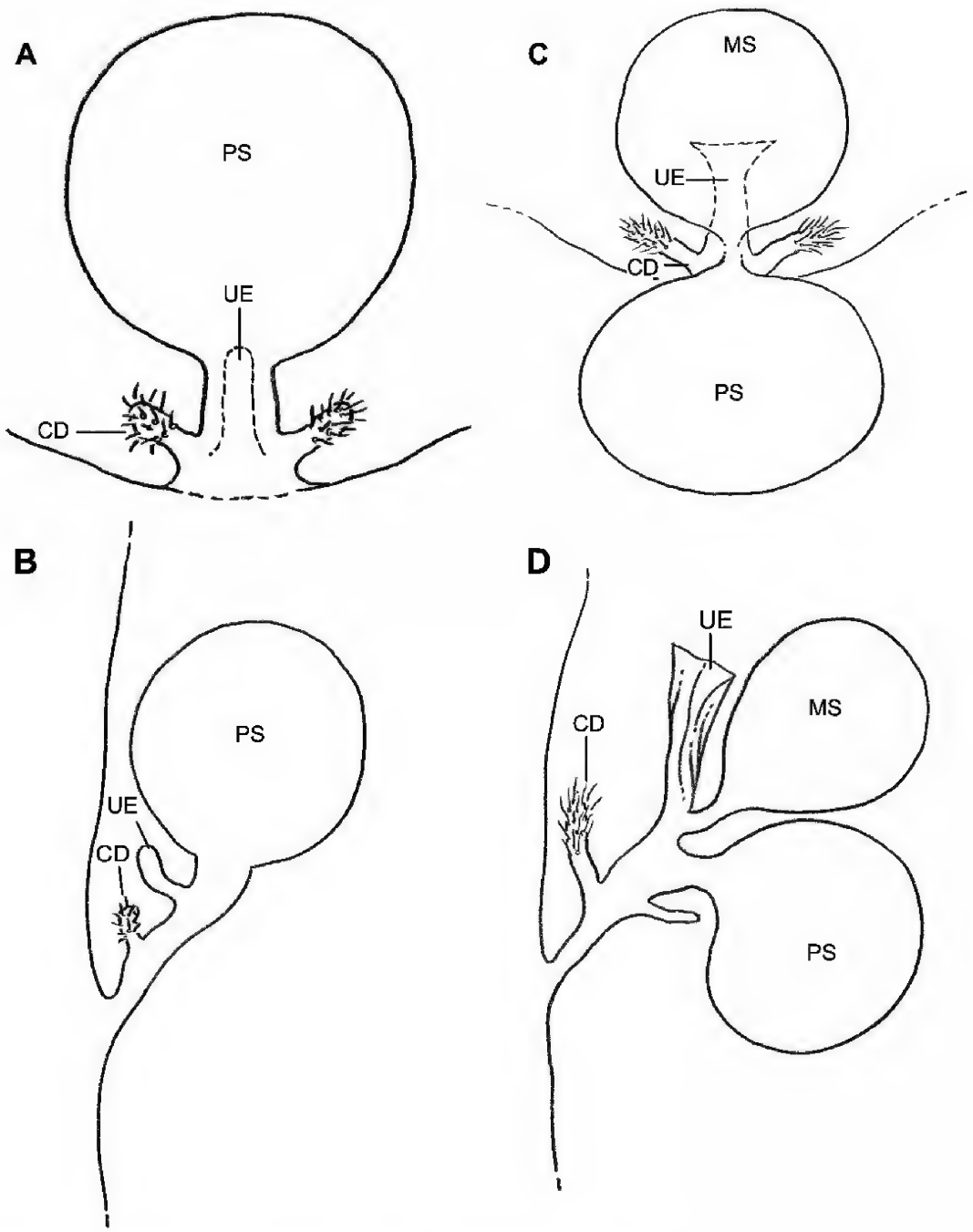

Fig. 7. Schematic representation of the internal female genitalia in *Cyrtognatha*. **A** (dorsal) and **B** (lateral) represent the case when median sac is not developed (e.g., *C. insolita*, *C. pachygnathoides*). **B** (dorsal) and **D** (lateral) represent the species that have median sac (e.g., *C. rucilla*, *C. espanola*, *C. simoni*). Dimitrov et al. (2007: fig. 10).

Spinnerets: ALS with extensive piriform fields of more than 45 spigots (figs. 28A, B, 35C,G). PLS mesal cylindrical spigot peripheral (figs. 28A, C, G, 35F). PLS with a line of macrosetae on its retrolateral surface (figs. 28A, G, J, 35E–F; such a line of setae is unique to *Cyrtognatha* and is one of the most conspicuous synapomorphies of this genus). PLS with about 15–20 AC spigots (fewer in males) arranged roughly in two transversal lines. The two CY spigots are placed retrolaterally, one anterior and the other posterior to the AC lines. In females the AG–FL triplet is just anterior to AC and on the same line with the anterior CY spigot. Both AG spigots embrace the FL spigot and the three of them are placed in a fairly straight line (figs. 28C–E, G, J, 35E–F). Adult males lack the triplet (fig. 57C). PMS in females with a large CY spigot with modified setae near its base (figs. 28H, 36A) on the anterior edge; AC spigots (10 or fewer) forming a straight line between the CY and the medially placed mAP (figs. 28F, H, 36A). In males PMS does not have the CY spigot and the number of the AC spigots is less than in females (fig. 57B). In both males and females PMS have well-developed nubbin posteriorly to the mAP (figs. 57B and 28H, respectively).

Tracheal system simple (figs. 41H, I, 45E, F): Tracheal spiracle situated near the spinnerets. There are two shorter median and two longer lateral tracheae, which are not fused at the base and connect to an atrium that opens to a spiracle. The long pair of lateral tracheae enters the cephalothorax, while the short one barely reaches the anterior part of the abdomen. None of the tracheae has ramifications. The base of the tracheae carries numerous accessory glands (fig. 45G).

Male pedipalp (fig. 6): Tibia longer than wide, with six retrolateral trichobothria (figs. 8B, 37B) and long dark setae starting near its distal margin. Cymbium wider basally, elongated with swollen apex (figs. 13D, 27A, B, E, F). Base of the cymbium with a short conical apophysis, which seems to guide the movement of the paracymbium when the palp is expanded. Paracymbium almost straight or slightly curved with wider apex; not a separate sclerite, its inner part attached to the cymbium by a membrane, which allows certain mobility when filled with hemolymph (fig. 41D, F). Tegulum spherical. Embolus enlarged, often much larger than conductor. In some species the embolus has a subterminal enlargement of the spermatic duct (e.g., C. *morona*; fig. 16A–C). Embolus base arising from center of tegulum and coiling then with conductor. Portion of the embolus enclosed in conductor varies between species but in all cases most of it is free (e.g., *C. atopica* and *C. rucilla*; figs. 8A–C and 41A–C, respectively). Apical part of tegulum with a cuplike depression where the embolus and the conductor rest; the edge of this depression is slightly elevated, forming a small ridge. In some species this ridge is heavily chitinized and has brownish coloration. Apical part of the tegulum membranous, connecting to the embolus base and conductor by means of a membrane (this membranous connection allows limited mobility of the embolus and the conductor with respect to the tegulum). Sperm duct starts from the wide fundus and coils 1.5–2 times before exiting the tegulum near its center. The last half turn of the spermatic duct, just before exiting the tegulum, abruptly narrows, decreasing its diameter by more than two-thirds (figs. 6A, D, E, 41D–F, 62D).

Embolus in most of species with a very well developed and complex metine embolic apophysis (MEA, figs. 6A, B, D, 13A, C, F, 62D). A large and complex membrane is often present between the outer heavily chitinized part of the MEA and the embolus. In some species this membrane connects to the embolus near the base of the MEA and runs to its tip forming various folds (fig. 13A). Although most of the species have a MEA of varying complexity, in several species the embolus does not have any apophyses (e.g., *C. rucilla* and *C. simoni*; figs. 41A–C, 43B, J, H and fig. 47A–C, respectively) or has small longitudinal ridges (e.g., *C. paradoxa*; fig. 20A–C). In *C. insolita* the membrane between the MEA and the embolus is densely covered with short conical outgrowths (fig. 39I, J), giving this membrane a serrated appearance. Similar outgrowths, but with lower density and different shape, are found in other species (e.g., *C. quichua*, fig. 13F, I). Apical part of the embolus very variable across species and

therefore useful for identification. Embolus tip always cylindrical, independent of the shape of the rest of the embolus. In some species the embolus tip carries a small membranous ridge (e.g., *C. bella*; fig. 58A–C). In addition to this membranous ridge *C. morona* has also a short apophysis (fig. 16A–C).

Conductor (fig. 6) originating from the tegulum as a single lamina that bends toward the center of the tegulum and goes under the basal part of the embolus. In this area the conductor lamina has a long lamellar process, the basal conductor apophysis that runs apically over the tegulum and under the embolus (fig. 6C). Distal edge of basal conductor apophysis continues on prolateral side of embolus and turns apically. In many species the basal conductor apophysis ends with a well-developed membrane or with an incision that forms two processes. Distal to the base of the basal apophysis the conductor bends again but in the opposite direction, partially covering the embolus. The tip of the conductor in all species of the genus has a very characteristic semicircular apical apophysis (figs. 6A, C–E, 9A, 41A). Epiandrous fusules arranged in a line in a shallow invagination of the cuticle just over the male gonopore (figs. 38G, 55D). The number of fusules varies between species from 6 in *C. insolita* (fig. 38G) to 14 in *C. bryantae* (fig. 55D). The morphology of the epiandrous fussles in most *Cyrtogantha* species, however, remains unknown, and thus the variation may be wider.

Females lack epigynum. The opening of the female genitalia is formed by a fold of the abdomen cuticle that carries setae on its dorsal side (the actual genital opening is shifted to the end of this fold; fig. 7). Spermathecae absent or vestigial. The uterus externus connects via an enlarged chamber with a nonpaired membranous structure that has a posterior sac (a nonpaired sperm storage organ) (see also Dimitrov et al., 2007).

COMPOSITION: *Cyrtognatha* currently contains 21 species: *C. nigrovittata* Keyserling, 1881, *C. pachygnathoides* (O. P.-Cambridge, 1894), *C. bella* (O. P.-Cambridge, 1896), *C. serrata* Simon, 1897, *C. lepida* (O. P.-Cambridge, 1889), *C. simoni* (Bryant, 1940), *C. rucilla* (Bryant, 1945), *C. espanola* (Bryant, 1945), *C. bryantae* (Chickering, 1956), *C. insolita* (Chickering, 1956), *C. catia*, n. sp., *C. atopica*, n. sp., *C. eberhardi*, n. sp., *C. quichua*, n. sp., *C. waorani*, n. sp., *C. morona*, n. sp., *C. leviorum*, n. sp., *C. petila*, n. sp., *C. paradoxa*, n. sp., *C. orphana*, n. sp., and *C. pathetica* n. sp.

Most of the species are known from just a few specimens. Given the wide distribution of this genus and the lack of extensive sampling in most of the Neotropical cloud forests, these species most likely represent just a small fraction of the true diversity of *Cyrtognatha*.

Cyrtognatha catia, new species
Figure 8

TYPE: Male holotype from Colombia, Cali, Valle del Cauca, San Antonio (near El Saladito), 3°29′49.2″N, 76°37′29.1″W, 2085 m elevation. 16.ii.1998, G. Hormiga, J. Coddington, J. Zujko-Miller, and D. Correa (USNM).

ETYMOLOGY: Named after the Catíos, the indigenous people living in Cauca Valley (Colombia) before the arrival of the Europeans. The species name is a noun in apposition.

DIAGNOSIS: Easily distinguished from similar congeners (*C. quichua* and *C. pachygnathoides*) by the shape of the embolus, which in ventral view is shaped as double S (fig. 8A) and is conspicuously curved in lateral view (fig. 8B, C). Further distinguished from *C. pachygnathoides* by the reduced membrane between the metine embolic apophysis and the embolus and the cylindrically shaped distal part of the embolus (fig. 8A–C). In *C. pachygnathoides* the embolus widens distally subapically and has a laminar shape. In *C. quichua* the embolus and the metine embolic apophysis are very similar but the embolus carries a semimembranous ridge that reaches to its tip (figs. 11A, 12D).

DESCRIPTION: *Male* (*holotype*). Habitus as in figure 8D–G. Carapace yellow-brownish with a well-marked fovea. Abdomen yellowish with numerous guanine spots and a short dorsal tubercle distally. Total length 4.75. Cephalothorax 2.25 long, 1.32 wide, 0.95 high. Abdomen 2.50 long, 1.18 wide, 1.25 high. Sternum 1.00 long, 0.87 wide. Clypeus

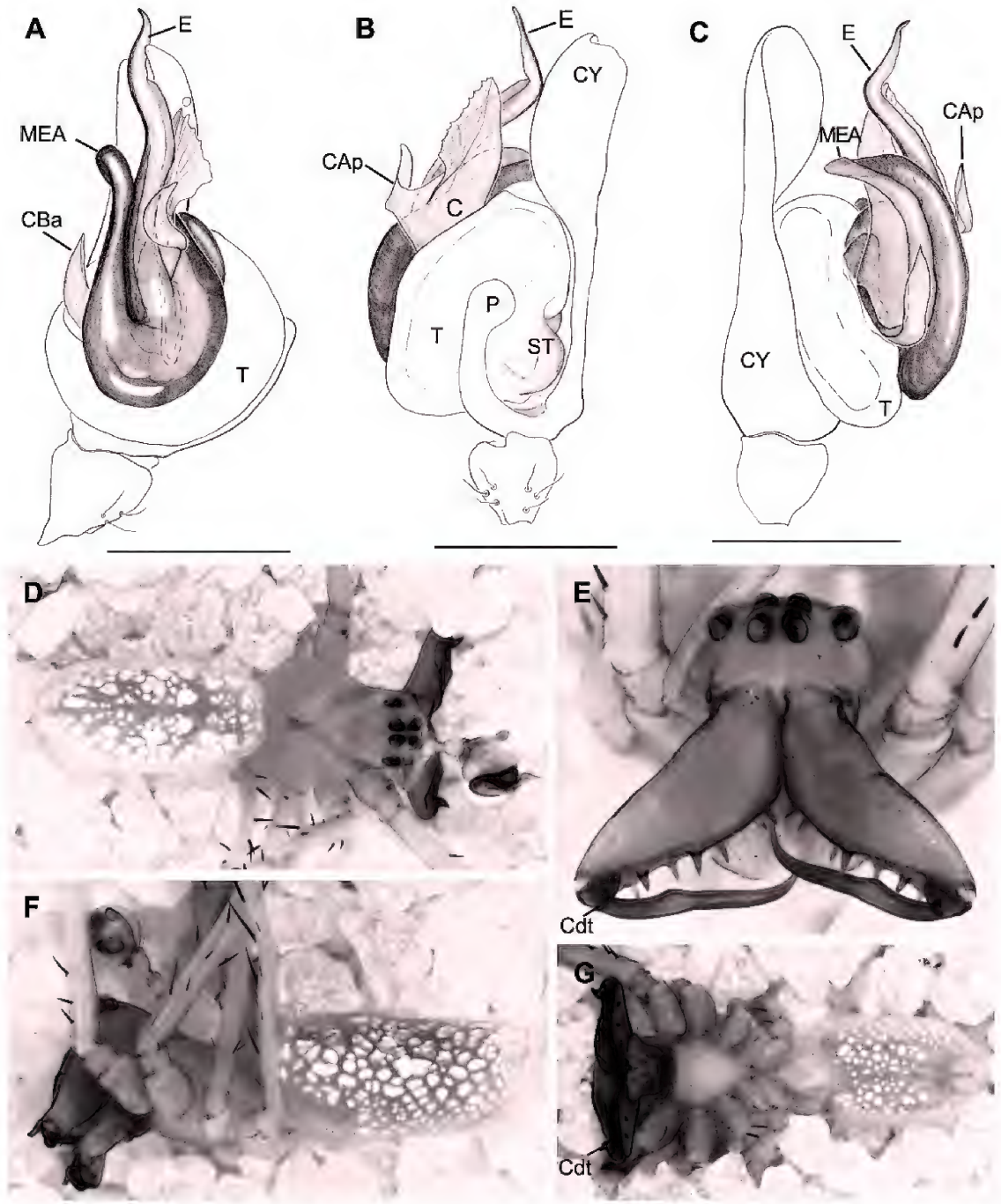

Fig. 8. *Cyrtognatha catia*, n. sp. Male palp: ventral (**A**), retrolateral (**B**), prolateral (**C**). Male habitus: dorsal (**D**), lateral (**F**), ventral (**G**). Male chelicerae (**E**). Scale bars 0.5 mm.

height 1.9 times one AME diameter. AME, ALE, and PLE almost the same size. AME diameter 0.1. PME slightly larger. Distance between PLE and PME twice the diameter of PME. ALE and PLE very close to each other. Distance between AME equal to their diameter; between PLE half of the PLE diameter. Chelicerae (fig. 8E) slightly darker

than the cephalothorax with large dorsal tooth distally situated very close to the joint of the cheliceral fang. Femur I 3.92, 1.74 times the length of the cephalothorax. Pedipalp as in figure 8A–C. Palpal tibia length 0.23; cymbium length 1.01.

Female. Unknown.

DISTRIBUTION: This species is known only from the type locality (fig. 5).

Cyrtognatha atopica, new species
Figure 9

TYPE: Male holotype from Argentina, Misiones, P. Prov. Cruce Caballero, San Pedro. Lat. 26.46667, long. 53.96667. 13–16.i.2005, Grismado, Lopardo, Piacentini, Quaglino, and Rubio (MACN).

ETYMOLOGY: The species epithet is an adjective and is derived from the Greek word *topikos* ("of a place, local") in reference to the unknown precise locality of the first specimen of this species examined by the authors.

DIAGNOSIS: Easily distinguished from other *Cyrtognatha* species by the morphology of the embolus and the conductor. Very large part of the embolus free; metine embolic apophysis ends as a long (almost as long as the embolus) curved lamina (fig. 9A–C). Apical apophysis of the conductor with a small outgrowth (fig. 9A) near its base. Distinguished from the very similar species *C. eberhardi* by the more globular tip of the paracymbium, the shape of the basal apophysis of the conductor, and the shape of the embolus (in *C. eberhardi* its tip is additionally curved so that the embolus end has an S shape). The basal apophysis of the conductor in *C. eberhardi* carries a long sharpened apophysis (fig. 10A), which is not present in *C. atopica*.

DESCRIPTION: *Male* (*holotype*). Habitus as in figure 9D–G. Carapace brown with a well-marked fovea. Abdomen brownish with silvery guanine spots. Distal tubercle extending dorsally over the spinnerets along the longitudinal axis of the abdomen. As a result of the orientation of its distal tubercle, the abdomen has cylindrical shape. Total length 5.39. Cephalothorax 1.96 long, 1.37 wide, 0.80 high. Abdomen 3.43 long, 0.93 wide, 0.73 high. Sternum with slightly clearer pigmentation in the center; 0.98 long, 0.93 wide. Clypeus height 1.4 times one AME diameter. Diameter of the AME 0.2. Distance between AME almost equal to their diameter and between them and ALE 1.5 times one AME diameter. Distance between AME and PME about one AME diameter. PME separated by distance nearly equal to their diameter. AME slightly larger than the rest of the eyes. Chelicerae (fig. 9E) brown with dorsal tooth distally outlying from the joint of the cheliceral fang. Femur I 4.9, 2.5 times the length of the cephalothorax. Pedipalp as in figure 9A–C. Palpal tibia length 0.30; cymbium length 1.08.

Female. Unknown.

DISTRIBUTION: The "S. A." abbreviation on the label of the second specimen most probably refers to South America. It is evident that based on this information alone it is impossible to determine very accurately the exact locality beyond the fact that it was collected somewhere in Brazil (fig. 5). The other known locality for this species is the Misiones province in the north of Argentina close to the boundary with Brazil.

ADDITIONAL MATERIAL EXAMINED: BRAZIL: S. A. (South America), Nathan Banks, 1 male (MCZ 66541).

Cyrtognatha eberhardi, new species
Figure 10

TYPE: Male holotype from Brazil, São Paulo, Fazenda Intervales, 15 km E of Guapiara, 700 m. xi.1990, W. Eberhard (MCZ 67457).

ETYMOLOGY: Named after William G. Eberhard, collector of many undescribed araneoid species, including the only known specimen of this species. The species name is a noun in the genitive case.

DIAGNOSIS: As in *C. atopica*, a very large part of the embolus is free and the metine embolic apophysis is long and laminar. These two characteristics clearly differentiate *C. eberhardi* from most species in the genus. The only species that has a similarly shaped metine embolic apophysis is *C. atopica*. *C. eberhardi* can be easily distinguished from the latter species by its more elongated paracymbium tip, the S-shaped tip of the embolus, and the shape of the basal apophysis of

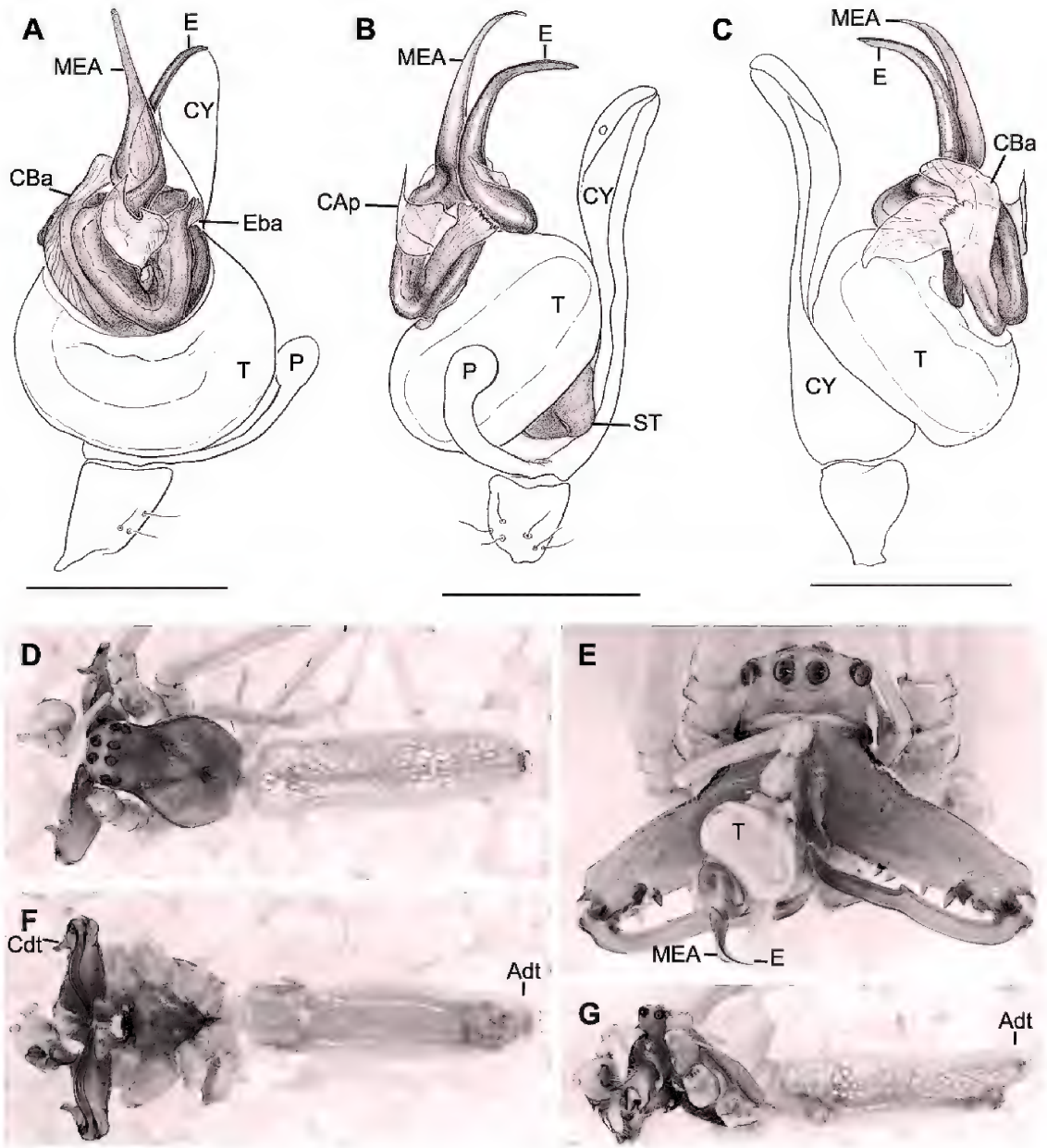

Fig. 9. *Cyrtognatha atopica*, n. sp. Male palp: ventral (**A**), retrolateral (**B**), prolateral (**C**). Male habitus: dorsal (**D**), lateral (**F**), ventral (**G**). Male chelicerae (**E**). Scale bars 0.5 mm.

the conductor (which in *C. atopica* has a long and sharpened apophysis that is absent in *C. eberhardi*). It is further differentiated from *C. atopica* by the presence of a short membranous ridge on the base of the embolus (fig. 10C).

DESCRIPTION: *Male* (*holotype*). Habitus as in figure 10D–G. Carapace yellowish with dark brown edges. Fovea well marked, dark brown. Abdomen cylindrical with numerous guanine spots concentrated over its dorsal and lateral surfaces and a dorsal line running longitudinally, with several small ramifications without guanine. Ventrally almost without guanine spots. Proximal and distal abdominal tubercles well developed and

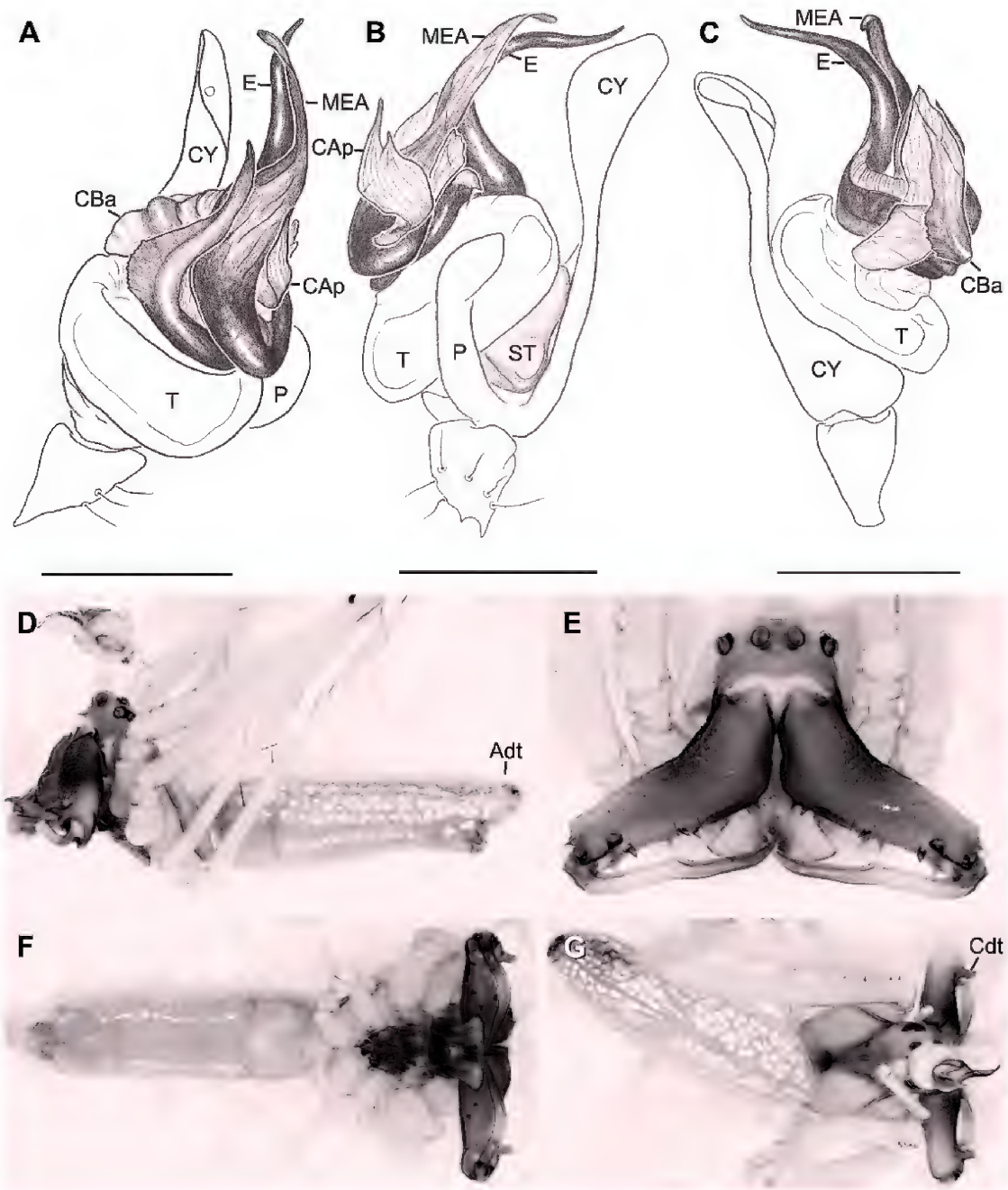

Fig. 10. *Cyrtognatha eberhardi*, n. sp. Male palp: ventral (**A**), retrolateral (**B**), prolateral (**C**). Male habitus: dorsal (**D**), lateral (**G**), ventral (**F**). Male chelicerae (**E**). Scale bars 0.5 mm.

oriented longitudinally. Total length 5.89. Cephalothorax 2.17 long, 1.50 wide, 0.87 high. Abdomen 3.72 long, 1.19 wide, 1.24 high. Sternum yellow-brownish with darker brownish pigmentation in the center and darker edges; 0.86 long, 0.80 wide. Clypeus height twice one AME diameter. Diameter of the AME 0.16. Distance between AME slightly less than their diameter; between AME and ALE 1.5 times one AME diameter.

Distance between PME about one PME diameter, PME–AME distance equal to one AME diameter. The lateral eyes juxtaposed and surrounded by a darker pigmentation. PME also surrounded by darker colored areas. AME slightly larger than the rest of the eyes and surrounded by slightly pigmented area. Chelicerae (fig. 10E) dark brown, very divergent, and with very well-developed dorsal cheliceral tooth. Dorsal tooth clearly outlying from the joint of the fang and curved at the tip prolaterally. Femur I 4.77, 2.1 times the length of the cephalothorax. Pedipalp as in figure 10A–C. Palpal tibia length 0.35; cymbium length 1.10.

Female. Unknown.

DISTRIBUTION: Known only from the type locality (fig. 5).

Cyrtognatha quichua, new species
Figures 1A–C, E, 3A, 11–14

TYPE: Male holotype from Ecuador, Napo Province, San Isidro, reserva Sierra Azul, 00°40′S, 077°55′W, 2300 m. 12.vi.1996, T.E. Erwin, fogging sample no. 1361 (USNM).

ETYMOLOGY: Named after the Quichua, the major indigenous group in Ecuador. To be treated as a noun in apposition.

DIAGNOSIS: This species is very similar to the closely related species *C. catia* and *C. pachygnathoides*. It can be easily distinguished from *C. pachygnathoides* by the shape of the embolus, which is not widened subterminally. In *C. catia* the embolus is not widened but it is shaped as an "S" in ventral view (fig. 8A), while in *C. quichua* the embolus gradually curves toward the cymbium. *C. quichua* can be further distinguished from similar congeners by the presence of a semimembranous ridge on the embolus that reaches its tip (figs. 11A, 12D, 13A, C). The morphology of the male chelicerae is also very diagnostic. *C. quichua* has the strongest and the most divergent chelicerae compared to the other two species (figs. 11G, 12C).

DESCRIPTION: *Male* (*holotype*). Habitus as in figures 1A–C, 11G, H, 12A, B. Carapace brownish with a well-marked fovea. Abdomen brown-yellowish with numerous guanine spots and a conspicuous dorsodistal tubercle. Total length 4.50. Cephalothorax 2.45 long, 1.86 wide, 0.98 high. Abdomen 2.10 long, 1.57 wide, 1.96 high. Sternum 1.00 long, 0.98 wide. Clypeus height twice an AME diameter. All eyes nearly the same size except PME slightly larger. AME diameter 0.1. PLE–PME distance slightly more than twice one PME diameter. ALE and PLE juxtapose. Distance between AME equal to their diameter; between PLE half one PLE diameter. Chelicerae (figs. 11D, G, 12C, E, G) strong, slightly darker than the rest of the cephalothorax, with well-developed dorsal tooth distally. Dorsal cheliceral tooth curved, well developed, and very close to the joint of the fang. Femur I 4.90, twice the length of the cephalothorax. Epiandrous fusules as in figure 12F. Pedipalp as in figures 11A–C, 12D, 13A–F, I. Palpal tibia length 0.96; cymbium length 1.03. Male spinnerets as in figures 13A, B, G–H.

Female (*paratype from the type locality*). Coloration and general habitus as in male. Abdominal tubercle less developed than in male. Total length 8.33. Cephalothorax 3.43 long, 2.25 wide, 1.47 high. Abdomen 4.90 long, 1.56 wide, 4.00 high. Sternum 1.22 long, 1.21 wide. Clypeus height 1.3 times one AME diameter. Eyes as in male. AME diameter 0.09. Distance between PME equal to their diameter. Chelicerae less divergent than in male, with cheliceral teeth closer to each other. Femur I 5.29, 1.54 times the length of the cephalothorax. Vulva as in figure 11E, F. Median sac relatively small on the top of a high chamber.

Variation. Male cephalothorax ranges in length from 2.54 to 2.45 (n = 4). Female cephalothorax is nearly the same in the two specimens studied (3.43). Male total body length ranges from 4.50 to 6.96 (n = 4). Female total body length ranges from 7.35 to 8.33 (n = 2). The male abdominal tubercle varies in height; in some specimens it is as high as the abdomen. Guanine spots vary in size; in some specimens the spots cover almost entirely the lateral and dorsal sides of the abdomen.

DISTRIBUTION: This species is known only from the type locality (fig. 5).

NOTES: The coloration of the abdomen in live specimens is greenish with some darker brownish patches and numerous silvery guanine spots (fig. 1A–C). It seems that the pigment responsible for the green color in

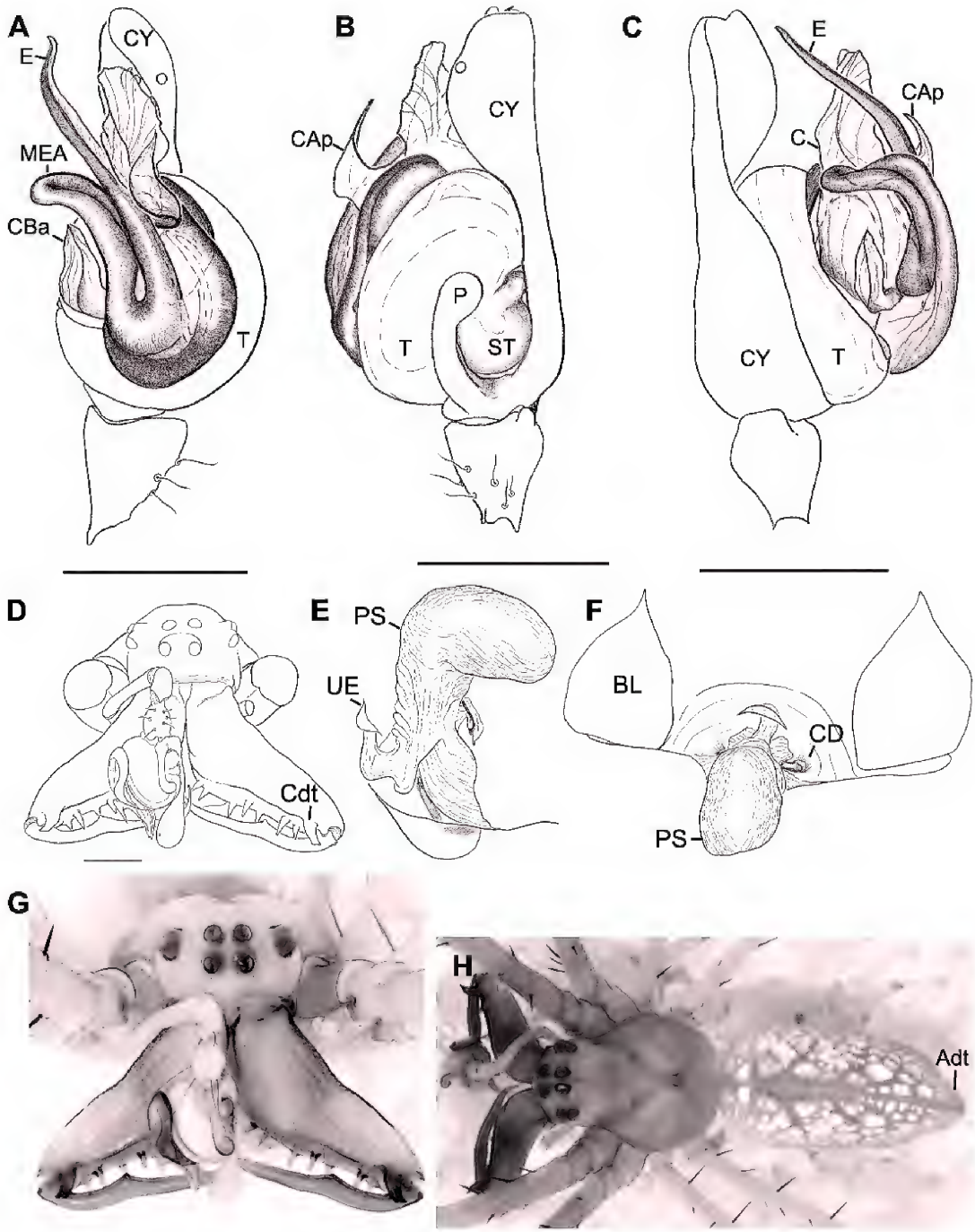

Fig. 11. *Cyrtognatha quichua*, n. sp. Male palp: ventral (**A**), retrolateral (**B**), prolateral (**C**). Male cephalothorax frontal (**D**). Vulva lateral (**E**), dorsal (**F**). Male habitus: frontal (**G**), dorsal (**H**). Scale bars A–E: 0.5 mm; F: 0.1 mm.

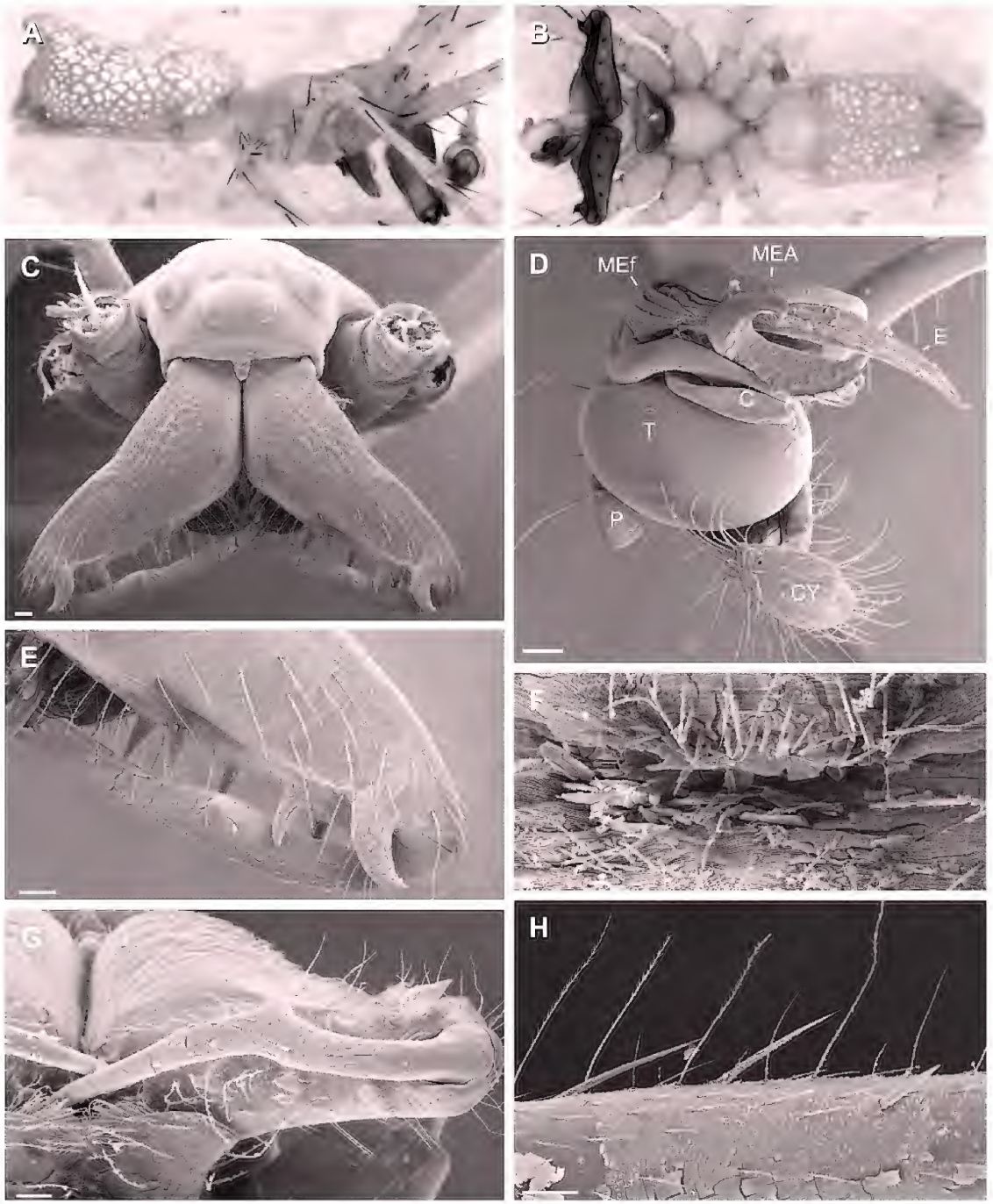

Fig. 12. *Cyrtognatha quichua*, n. sp. Male habitus: lateral (**A**), ventral (**B**). Male chelicerae (**C**, **E**, **G**). Male palp apical (**D**). Epiandrous fusules (**F**). Male leg IV femur (H). Scale bars C–E, G, H: 100 μm; F: 10 μm.

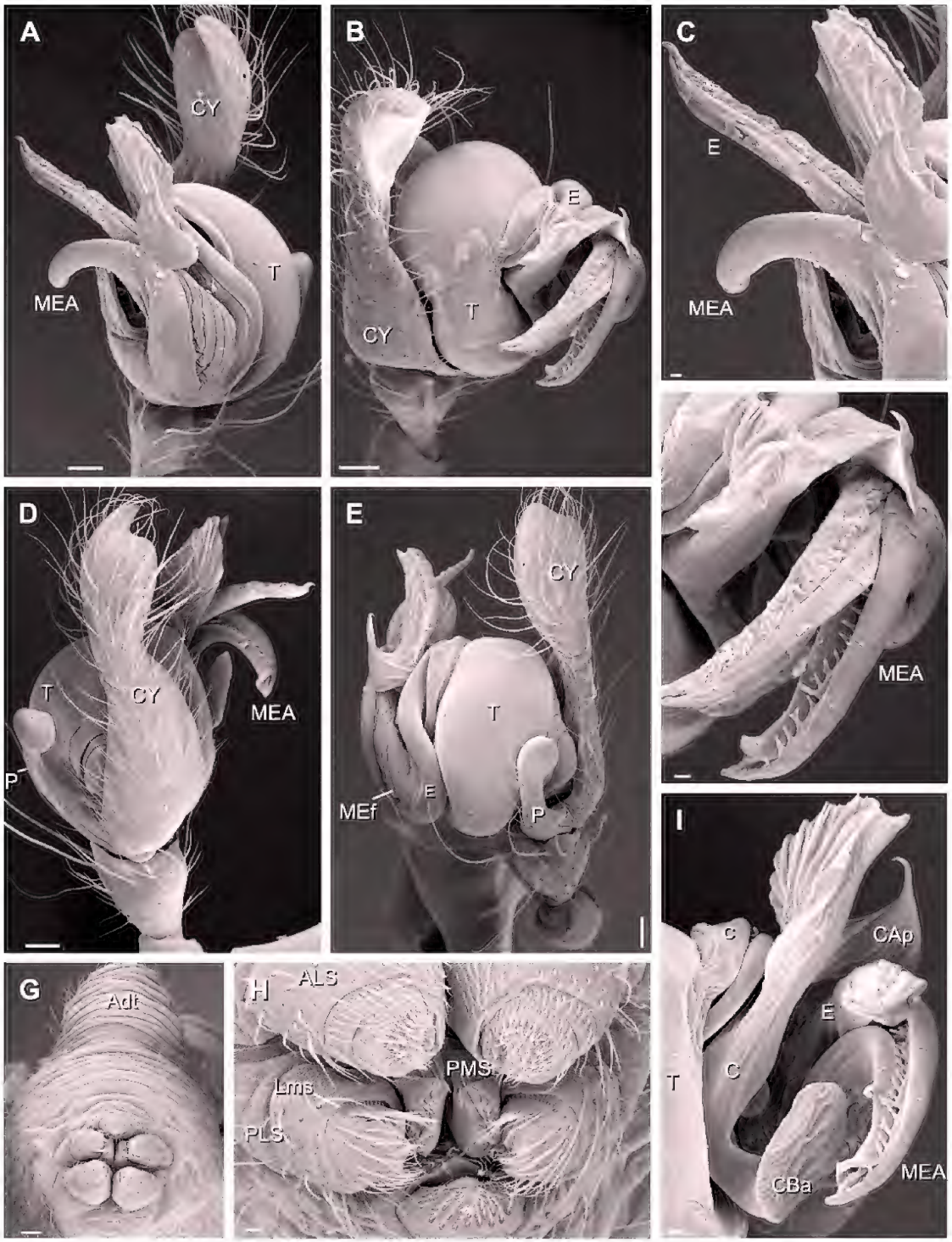

Fig. 13. *Cyrtognatha quichua*, n. sp. Male palp: ventral (**A**), lateral (**B**), embolus and MEA ventral (**C**), dorsal (**D**), retrolateral (**E**), MEA retrolateral (**F**), conductor and embolus prolateral (**I**). Male abdomen caudal (**G**). Male spinnerets ventral (**H**). Scale bars A, B, D, E, G: 100 μm; C, F, H, I: 20 μm.

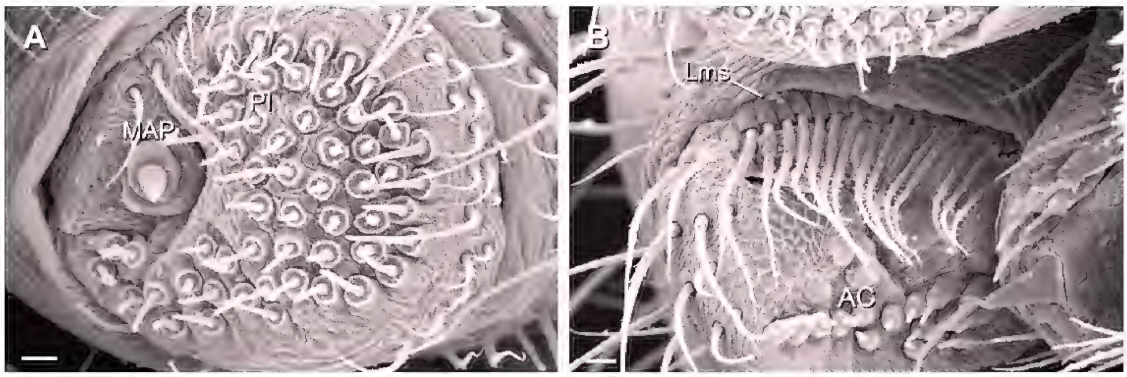

Fig. 14. *Cyrtognatha quichua*, n. sp. Male spinnerets: ALS (**A**), PLS (**B**). Scale bars 10 μm.

vivo degrades rapidly when the specimens are stored in alcohol.

ADDITIONAL MATERIAL EXAMINED: *Paratypes:* ECUADOR: Napo Province–Sierra Azul, 00°40′S, 077°55′W, 2300 m. 1 female, 12.vi.1996, T.E. Erwin, fogging sample no. 1361 (USNM); same locality, 13–15.vi.1996, G. Hormiga, 1 male (SEM); same locality, 15.vi.1996, G. Hormiga, 1 male; same locality, 13.vi.1996, G. Hormiga, 1 male, 1 female.

Cyrtognatha waorani, new species
Figure 15

TYPE: Male holotype from Ecuador, Orellana, Reserva Étnica Waorani, Transect Ent. 1 km S. Onkone Gare Camp. 00°39′25.7″S, 076°27′10.8″W, elevation 216 m. 9.x.1994, T.L. Erwin et al., lot no. 915 (USNM).

ETYMOLOGY: Named after the Waorani people, an indigenous tribe of the Ecuadorian Oriente in the Amazon region. The species name is to be treated as noun in apposition.

DIAGNOSIS: This species can be easily distinguished from similar congeners (namely, *C. orphana*) by the very peculiar shape of the metine embolic apophysis (fig. 15A, C), which is widened and with a deep distal incision. *Cyrtognatha orphana* has a similarly shaped metine embolic apophysis, but its embolus has a smaller embolic membrane and is conspicuously bent (in ventral view) prolaterally. In *C. morona* the embolus has S curvature and its tip points apically (fig. 15A). The extensive membrane of the embolus and the shape of the basal apophysis of the conductor are also very useful for the identification of *C. waorani* (fig. 15A–C).

DESCRIPTION: *Male* (*holotype*). Habitus as in figure 15D–G. Carapace brown-yellowish with a well-marked fovea. Abdomen brownish with numerous guanine spots concentrated dorsally and laterally. Dorsal tubercle extends caudally over the spinnerets and has darker bands. Total length 6.00. Cephalothorax 2.80 long, 1.90 wide, 1.36 high. Abdomen 3.26 long, 0.90 wide, 0.78 high. Sternum 0.93 long, 1.17 wide. Clypeus height 1.25 times one AME diameter. AME and PME almost the same size. AME diameter 0.13. Lateral eyes juxtaposed and slightly smaller than PME, distance between ALE and AME more than 1.5 AME diameters. Distance between AME slightly larger than their diameter. Distance between PME about two-thirds of their diameter. Chelicerae (fig. 15E) brownish, with very well-developed dorsal tooth close to the fang joint. Fang with very pronounced curvature and outgrowth over its retrolateral surface. Tip of the dorsal cheliceral tooth conspicuously curved; the rest of the cheliceral teeth rather small. Femur I 6.82, 2.4 times the length of the cephalothorax. Pedipalp as in figure 15A–C. Palpal tibia length 0.22; cymbium length 0.97.

Female. Unknown.

DISTRIBUTION: This species is known only from the type locality (fig. 5).

Cyrtognatha morona, new species
Figure 16

TYPE: Male holotype from Ecuador, Morona Santiago, 3.0093S, 78.4939W, elevation 1750 m. 12.vii.2004, Maddison, Agnarsson, Iturralde, and Salazar (MCZ).

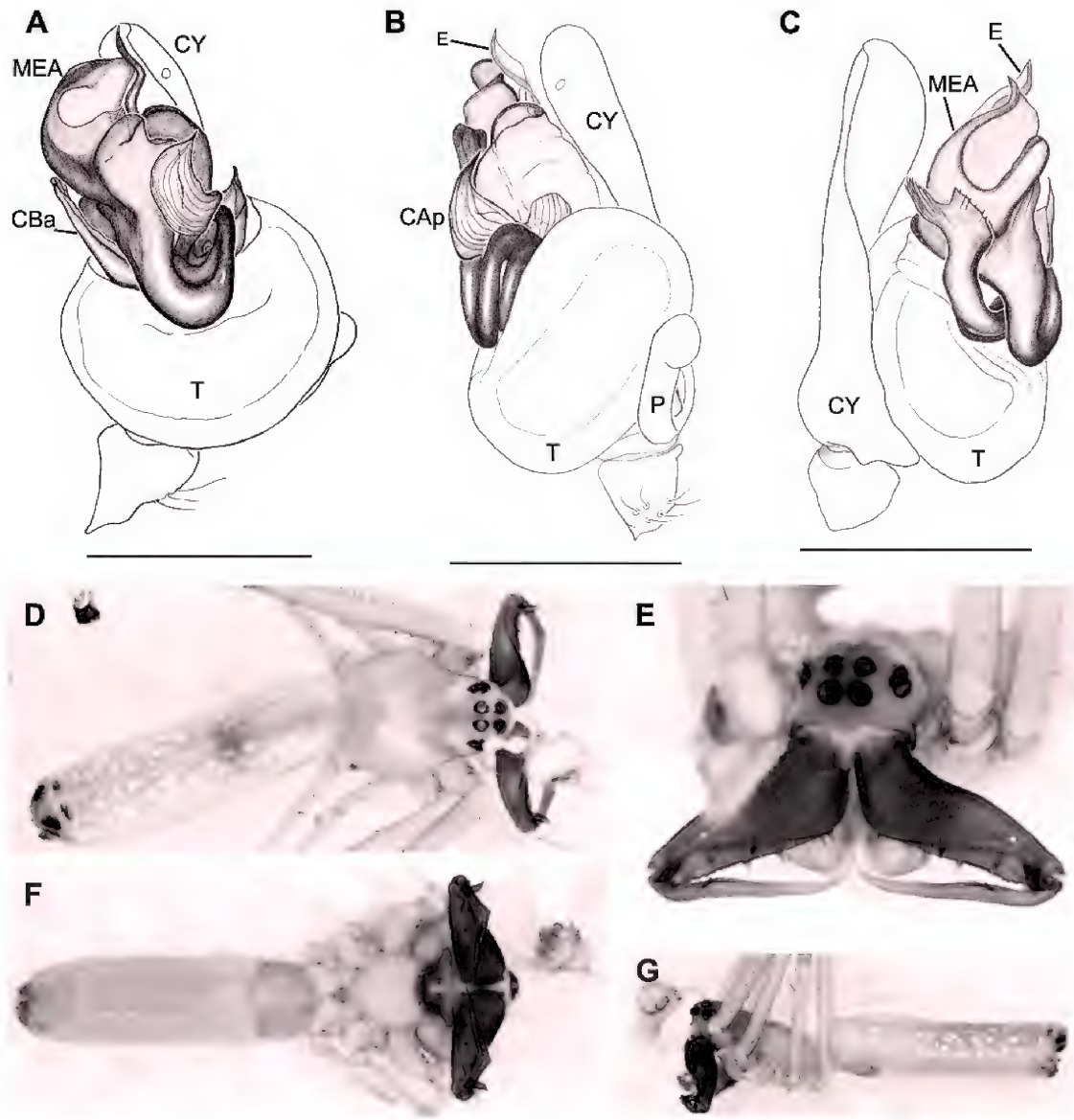

Fig. 15. *Cyrtognatha waorani*, n. sp. Male palp: ventral (**A**), retrolateral (**B**), prolateral (**C**). Male habitus: dorsal (**D**), ventral (**F**), lateral (**G**). Male chelicerae (**E**). Scale bars 0.5 mm.

ETYMOLOGY: The species epithet is a name in apposition taken from the type locality.

DIAGNOSIS: *Cyrtognatha morona* can be easily distinguished from all other *Cyrtognatha* species by the presence of a very conspicuous apophysis on the top of the embolus (fig. 16A–C). The overall shape of the embolus is also very diagnostic (fig. 16A–C).

DESCRIPTION: *Male* (*holotype*). Habitus as in figure 16D–G. Carapace yellowish with a well-marked fovea and darker band running longitudinally. Carapace margins with darker grayish bands. Legs greenish, darker than the cephalothorax. Abdomen cylindrical, with small tubercles. Tip of the dorsal tubercle oriented caudally. Abdomen with gray-greenish coloration and with numerous guanine spots concentrated in two dorsolateral bands. Central part of the abdomen dorsally with darker greenish coloration and without

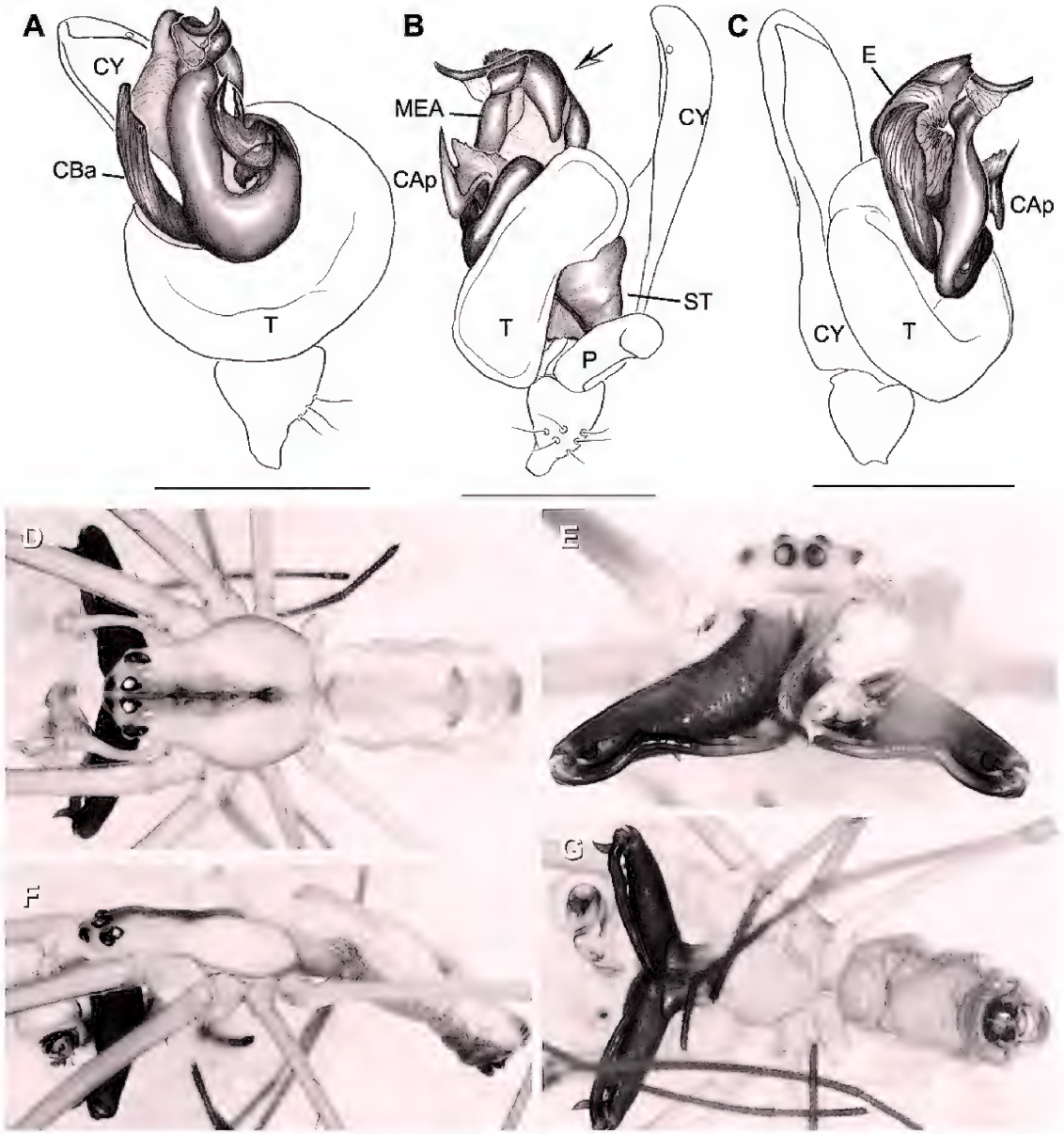

Fig. 16. *Cyrtognatha morona*, n. sp. Male palp: ventral (**A**), retrolateral (**B**), prolateral (**C**). Male habitus: dorsal (**D**), ventral (**F**), lateral (**G**). Male chelicerae (**E**). Scale bars 0.5 mm. Arrow points to the apical embolic apophysis.

guanine. Ventrally the epigastric furrow well marked, brownish in color, and strongly chitinized. Spinnerets coloring darker and brownish. Total length 4.75. Cephalothorax 2.00 long, 1.43 wide, 0.88 high. Abdomen 2.75 long, 1.00 wide, 0.88 high. Sternum yellowish with greenish tones and darker edges, 0.93 long, 0.85 wide. Endites and labium darker with brown pigmentation. Clypeus height 1.7 times one AME diameter. Eyes nearly the same size. AME diameter 0.10. All eyes surrounded by darker brownish pigmentation. Lateral eyes over short elevations. ALE touch PLE. Distance between AME slightly less than their diameter; between AME and ALE at about 1.5 times

one AME diameter. PME separated by distance slightly shorter than PME diameter. Chelicerae (fig. 16E) dark brown, robust, and widely divergent. Dorsal cheliceral tooth very well developed, outlying the fang joint and curved prolaterally. Cheliceral fang with well-developed dorsal outgrowth. Femur I 4.65, 2.32 times the length of the cephalothorax. Pedipalp as in figure 16A–C. Palpal tibia length 0.27; cymbium length 0.95.

Female. Unknown.

DISTRIBUTION: Known only from the type locality (fig. 5).

Cyrtognatha leviorum, new species
Figure 17

TYPE: Male holotype from Panama, Chiriquí Province, Boquete, above 1200–1900 m. 11.vii.1983, H. and L. Levi (MCZ 67465).

ETYMOLOGY: Named after Herbert W. Levi and Lorna R. Levi, collectors of the only known specimen of this species and in recognition of H. W. Levi's work on the systematics of Neotropical araneoids. The species name is a noun in the genitive case.

DIAGNOSIS: This species is very similar to its closest relative, *C. bella*. It can be easily distinguished from *C. bella* by the morphology of the embolus, which in *C. leviorum* has smaller dilatation ventrally and carries a small metine embolic apophysis (fig. 17A). In *C. bella* the embolus does not have a metine embolic apophysis. The male chelicerae are also diagnostic: in *C. bella* they are more divergent with much larger outgrowth of the cheliceral fang (fig. 58E) than in *C. leviorum* (fig. 17E). Additional diagnostic characters are provided by the more rounded tip of the paracymbium and more pronounced curvature of the embolus (in prolateral view) in *C. leviorum*.

DESCRIPTION: *Male* (*holotype*). Habitus as in figure 17D–G. Carapace yellowish with a well-marked fovea. Dorsally with darker brownish band medially. Abdomen cylindrical with well-developed proximal tubercle but with strongly reduced distal one. Abdomen yellowish in color with guanine spots concentrated dorsally. Total length 4.12. Cephalothorax 1.87 long, 1.32 wide, 0.87 high. Abdomen 2.25 long, 1.25 wide, 1.00 high. Sternum yellowish, 0.95 long, 0.90 wide. Clypeus height 1.36 times one AME diameter. Eyes nearly the same size. AME diameter 0.11. Distance between AME slightly smaller than their diameter; AME–ALE distance twice one AME diameter. Distance between PME equal to their diameter, and PME–AME distance ca. 1.5 AME diameters. Chelicerae (fig. 17E) brownish, moderately divergent with a well-developed dorsal tooth. The dorsal tooth is placed near the fang articulation (fig. 17E), carries a bunch of macrosetae, and is curved at the tip prolaterally. Cheliceral fang with very well-developed outgrowth but without very distinctive curvature before and after it. Femur I 3.72, 1.98 times the length of the cephalothorax. Pedipalp as in figure 17A–C. Palpal tibia length 0.27, cymbium length 0.72.

Female. Unknown.

DISTRIBUTION: Known only from the type locality (fig. 5).

Cyrtognatha petila, new species
Figures 3E, 18, 19

TYPE: Male holotype from Mexico, Chiapas, Ocosingo, Ejido Nueva Argentina, Laguna Miramar, Reserva de la Biosfera Montes Azules, 16°23′36.2″N, 91°14′29.6″W, MAP 150 m. 23–25.x.2005. F. Álvarez, L. Lopardo, and J. Castelo (CNAN).

ETYMOLOGY: The species epithet is an adjective taken from the Latin word *petilus* ("thin, slender"), in reference to the body size and shape of this species.

DIAGNOSIS: This species can be easily distinguished from similar relatives (*C. insolita* and *C. orphana*) by the presence of a well-developed membrane on the tip of the basal apophysis of the conductor (fig. 18C). In *C. insolita* this membrane is missing (fig. 37C) and in *C. orphana* the basal apophysis of the conductor is much wider distally (fig. 22C). *C. petila* can be further distinguished from *C. orphana* by the triangular shape of the metine embolic apophysis (fig. 18A, B) and from *C. insolita* by the lack of a serrated membrane of the embolus in prolateral view. Here the serrated membrane is seen in retrolateral view (fig. 18B).

An important diagnostic feature of this species is the morphology of the male chelicerae. In *C. orphana* and *C. insolita* the

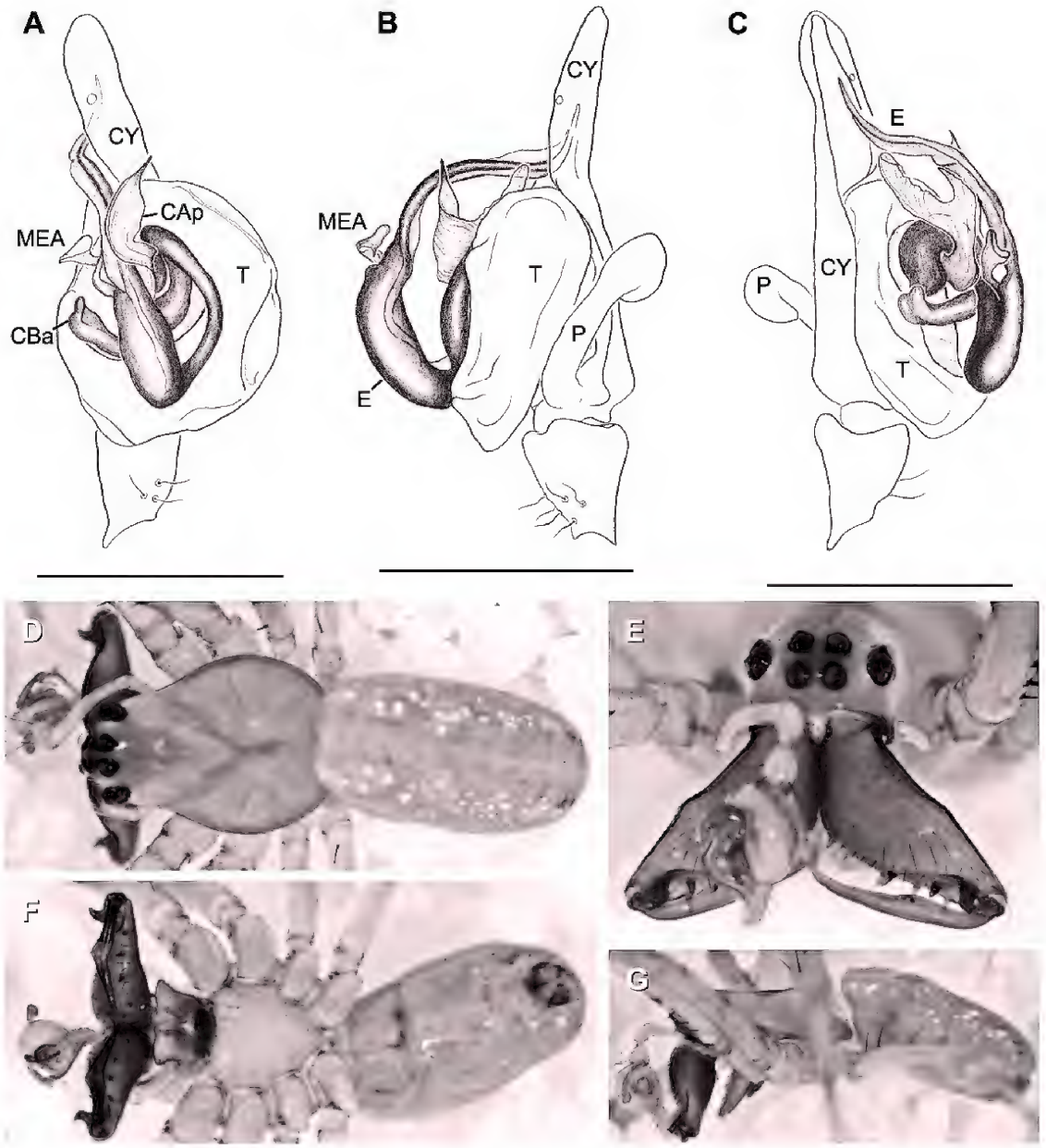

Fig. 17. *Cyrtognatha leviorum*, n. sp. Male palp: ventral (**A**), retrolateral (**B**), prolateral (**C**). Male habitus: dorsal (**D**), ventral (**F**), lateral (**G**). Male chelicerae (**E**). Scale bars 0.5 mm.

male chelicerae are much more divergent and with a very strong dorsal tooth (fig. 38B, E, F), while in *C. petila* the dorsal tooth is just slightly larger than the rest of the cheliceral teeth (fig. 19D).

DESCRIPTION: *Male* (*holotype*). Habitus as in figures 3E, 19A–D. Carapace yellowish with a well-marked fovea; with darker band in the center and darker margins. Dorsally some remains of greenish coloration still can be observed. Abdomen brown-grayish, cylindrical with guanine spots concentrated dorsolaterally. Ventrally and ventrolaterally with darker bands and with four darker spots on the distal edge dorsally. Abdominal tubercles strongly reduced. Total length 4.74. Cepha-

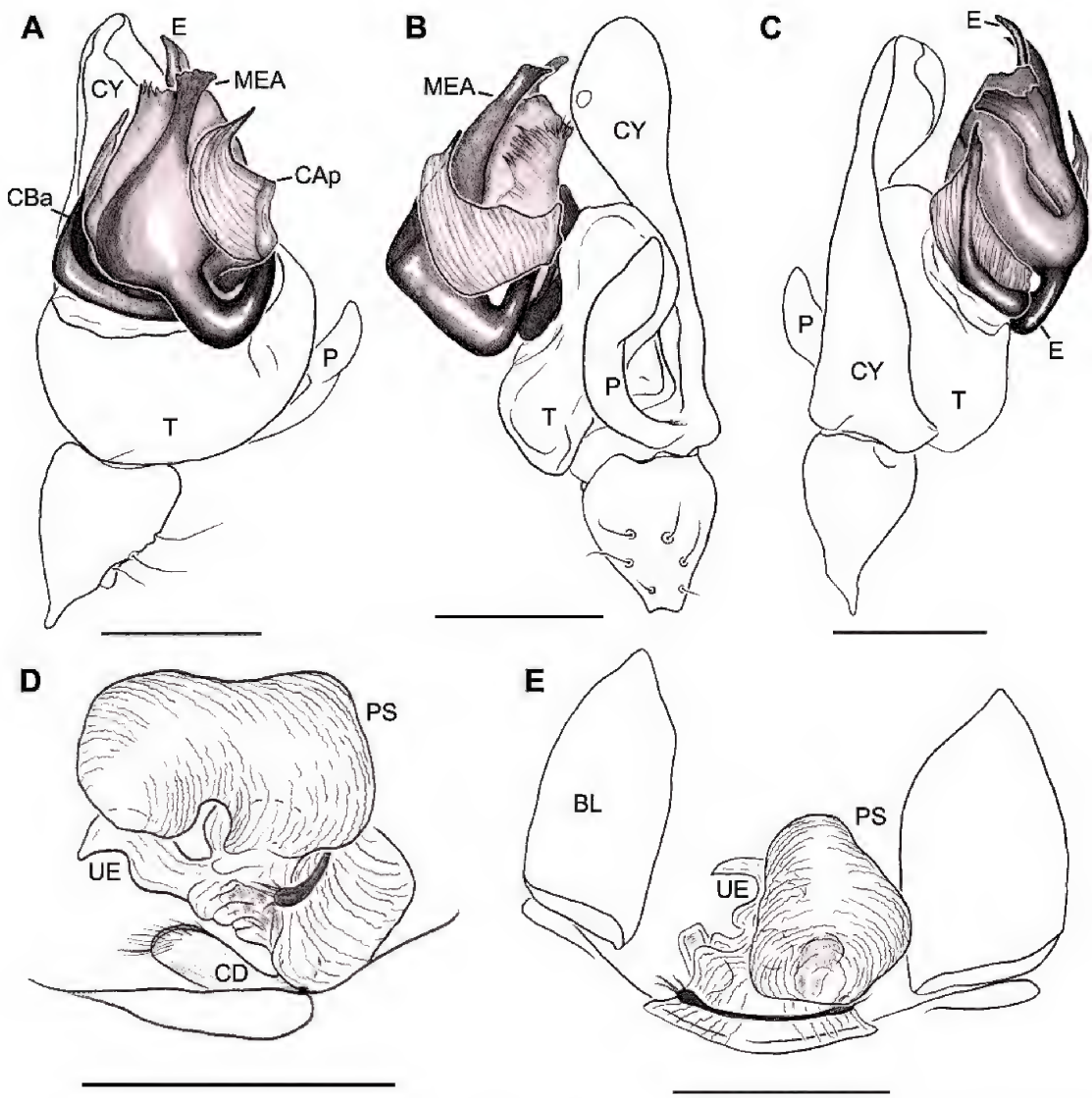

Fig. 18. *Cyrtognatha petila*, n. sp. Male palp: (**A**), retrolateral (**B**), prolateral (**C**). Vulva: lateral (**D**), dorsal (**E**). Scale bars A–C: 0.2 mm; D–E: 0.5 mm.

lothorax 1.74 long, 1.10 wide, 0.80 high. Abdomen 3.00 long, 0.80 wide, 0.70 high. Sternum yellowish with darker margins; 0.80 long, 0.78 wide. Clypeus height equal to an AME diameter. AME diameter 0.09. Distance between AME half of their diameter; ALE–PME distance 1.5 AME diameters and between them and PLE equal to one AME diameter. Distance between PME equal to their diameter. All eyes surrounded by dark pigmentation. Chelicerae (fig. 19D) moderately divergent with dark brown-grayish color. Dorsal cheliceral tooth well developed, outlying the fang joint and with sharp tip. Cheliceral fang with very strongly reduced outgrowth and practically straight except for the both edges. Femur I 4.03, 2.3 times the length of the cephalothorax. Pedipalp as in figure 18A–C. Palpal tibia length 0.2; cymbium length 0.54.

Female (*paratype from the type locality*). Habitus and coloration as in male. Chelicerae lack the dorsal tooth and are much less divergent. Sternum 0.90 long, 0.84 wide.

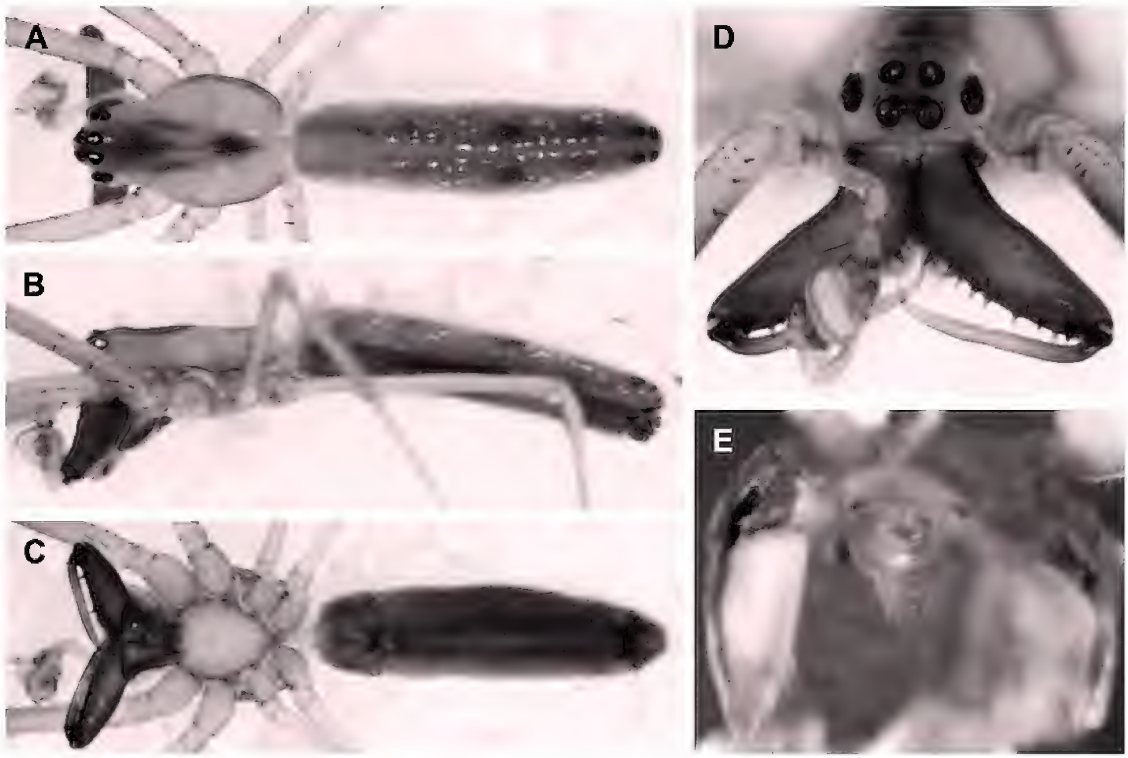

Fig. 19. *Cyrtognatha petila*, n. sp. Male habitus: dorsal (**A**), lateral (**B**), ventral (**C**). Male chelicerae (**D**). Vulva: dorsal (**E**).

Total length 7.39. Cephalothorax 2.12 long, 1.55 wide, 0.99 high. Abdomen 5.27 long, 1.67 wide, 2.17 high. Clypeus height half of one AME diameter. AME diameter 0.08. Femur I 5.33, 2.5 times the length of the cephalothorax. Vulva as in figures 18D, E.

Variation. Male cephalothorax ranges in length from 1.74 to 1.86 (n = 3). Female cephalothorax ranges in length from 1.96 to 2.12 (n = 9). Male total body length ranges from 4.74 to 5.38 (n = 3). Female total body length ranges from 6.16 to 7.39 (n = 9).

DISTRIBUTION: This species is known only from southern Mexico (Chiapas) (fig. 5).

ADDITIONAL MATERIAL EXAMINED: *Paratypes:* MEXICO: Chiapas, Ocosingo, Ejido Nueva Argentina, Laguna Miramar, Reserva de la Biosfera Montes Azules, 16°23′36.2″N, 91°14′29.6″W, MAP 150 m. 23–25.x.2005, F. Álvarez, L. Lopardo, and J. Castelo, 1 female (CNAN); Chiapas, Ocosingo, Sierra de la Cojolita, Arroyo Nayte. 16°47′36.2″N, 91°02′35.3″W, EPE 06 202 m. 1–27.x.2005, L. Lopardo, J. Castelo, and F. Álvarez, 2 female (CNAN); Chiapas, Ocosingo, Hidalgo Cortés orillas de la Reserva Montes Azules. N 16°42′19.1″N, 90° 53′08.2″W, EPE 07 145 m. 31.x.2005, L. Lopardo, J. Castelo, and F. Álvarez, 1 male and 5 females (CNAN); Chiapas, Ocosingo, Monumento Natural Bonampak, 16°43′32.5″N, 91°04′ 43.4″W, EPE07 207 m. 26.x–2.xi.2005, F. Álvarez, L. Lopardo, and J. Castelo, 1 female (CNAN).

Other material: MEXICO: Chiapas, Palenque ruins area. 92°01′W, 17°29′N. 2–11.vii.1983, W. Maddison and R.S. Anderson, 83-0995 tropical rain forest edge. 1 male (MCZ 67459).

Cyrtognatha paradoxa, new species
Figures 20, 21

TYPE: Male holotype from Mexico, Hidalgo, 4 km NE of Tlanchinol on Hwy. 105, 98°39′W, 21°02′N, ca. 1371 m. Cloud forest edge. 14.vi.1983, W. Maddison (MCZ 67463).

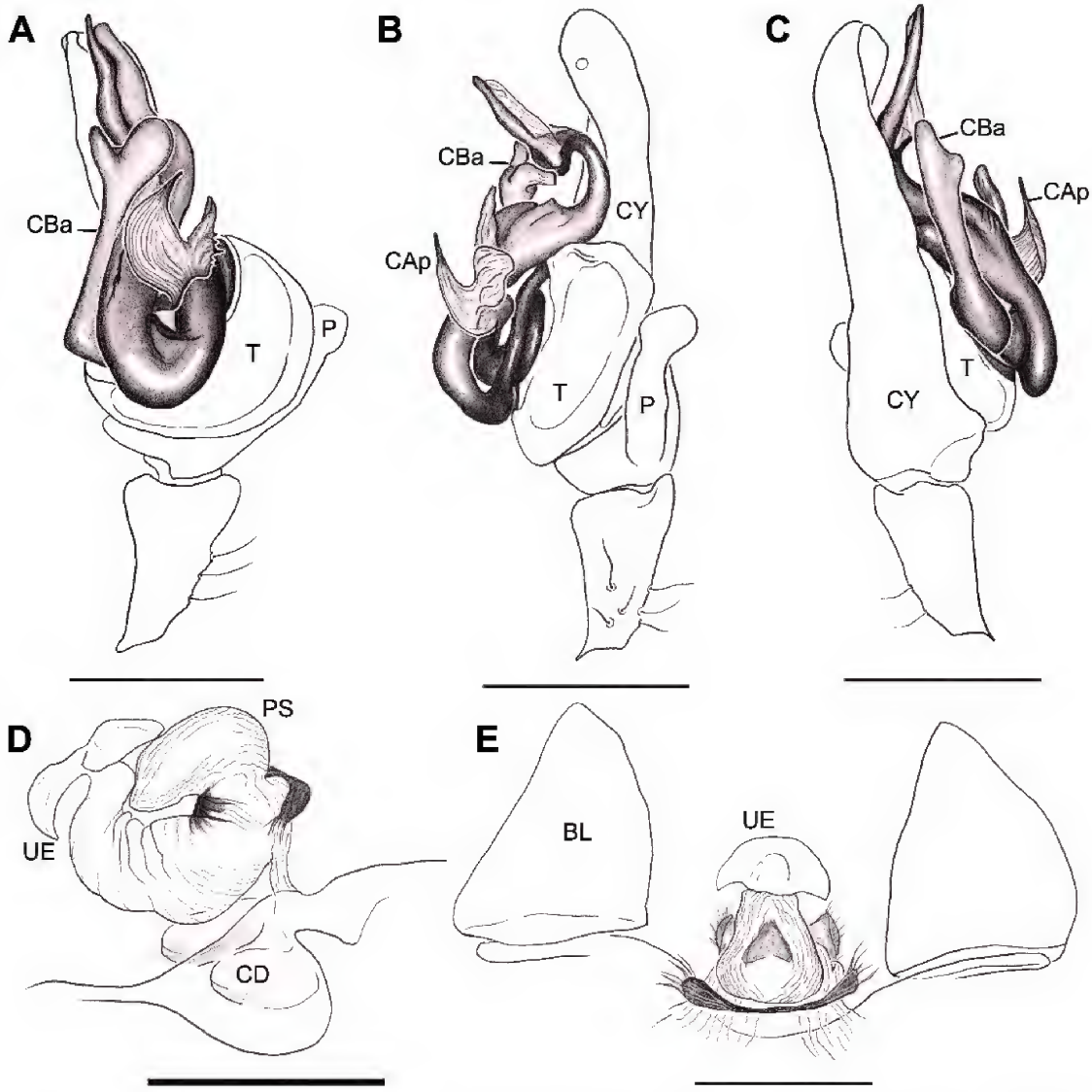

Fig. 20. *Cyrtognatha paradoxa*, n. sp. Male palp: (**A**), retrolateral (**B**), prolateral (**C**). Vulva: lateral (**D**), dorsal (**E**). Scale bars 0.5 mm.

ETYMOLOGY: The species epithet is an adjective that refers to the unusual male palp morphology.

DIAGNOSIS: This species can be easily distinguished from all other species in the genus by the very unusual shape of the basal apophysis of the conductor (fig. 20A–C). Here it is well developed, strongly chitinized, and carries two small outgrowths at the tip. It is easily distinguished from similar congeners by the shape of the embolus, which is conspicuously curved (fig. 20A–C) and carries a small membranous fold apically. The morphology of the apical apophysis of the conductor is also diagnostic (fig. 20A–B).

DESCRIPTION: *Male* (*holotype*). Habitus as in figure 21A–D. Carapace brown-yellowish, darker in the center and margins. Fovea well marked, darker. Abdomen cylindrical with guanine spots dorsally and laterally. Dorsally with darker bands. Distal and proximal tubercles small. Total length 6.82. Cephalothorax 3.10 long, 2.42 wide, 1.24 high. Abdomen 3.72 long, 1.74 wide, 1.36 high.

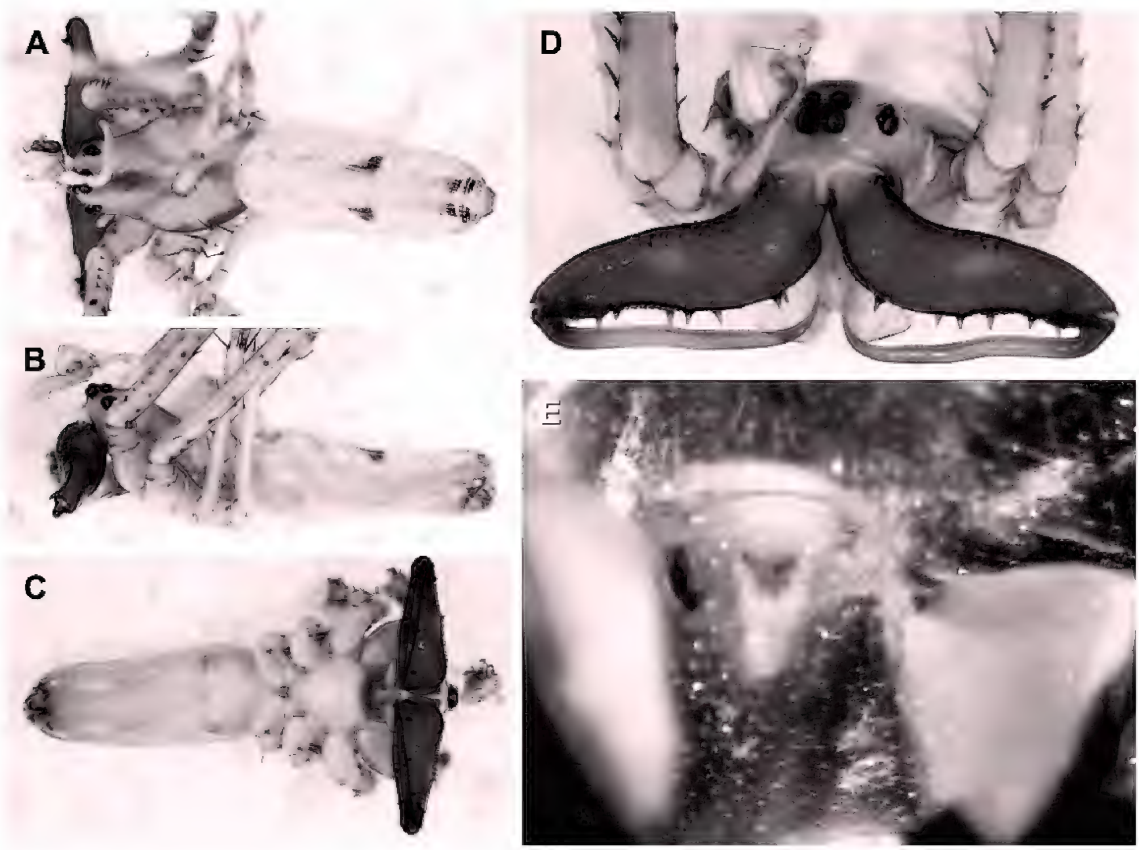

Fig. 21. *Cyrtognatha paradoxa*, n. sp. Male habitus: dorsal (**A**), lateral (**B**), ventral (**C**). Male chelicerae (**D**). Vulva: dorsal (**E**).

Sternum yellowish with darker bands between coxae; 1.24 long, 1.36 wide. Clypeus height 1.5 times one AME diameter. AME diameter 0.14. Distance between AME half of their diameter; AME–ALE distance slightly more than two AME diameters. PME close to each other and to the AME; distance between PME half of their diameter, PME–AME distance half of one AME diameter. AME and PME placed on well-marked bump. Lateral eyes on short tubercles. All eyes surrounded by a dark brown pigmentation. Chelicerae (fig. 21D) dark brown, strongly divergent with well-developed dorsal tooth. Dorsal tooth with pointed tip and outlying from the fang articulation. Chelicerae fang with reduced outgrowth and without distinctive curvature before and after the outgrowth. Femur I 6.20, twice the length of the cephalothorax. Pedipalp as in figure 20A–C. Palpal tibia length 0.55; cymbium length 1.17.

Female (*paratype from the type locality*). Coloration and habitus as in male. Abdomen damaged in the only specimen available for study, but the distal and proximal tubercles can be both distinguished and are more developed than in the male. Chelicerae less divergent than in male, without dorsal tooth; the rest of the cheliceral teeth well developed and closer to each other. Sternum 1.32 long, 1.25 wide. Clypeus height equal to an AME diameter. AME diameter 0.17. Eyes smaller than in males and placed on less pronounced elevations. Distance between AME and ALE equal to three AME diameters. Total length 8.86. Cephalothorax 3.90 long, 1.86 wide, 1.55 high. Abdomen 4.96 long. Abdomen width and height not measured (damaged specimen). Femur I 4.56, 1.3 times the length

of the cephalothorax. Vulva as in figures 20D, E, 21E.

DISTRIBUTION: This species is known from the southern Mexican states of Hidalgo and Veracruz (fig. 5).

ADDITIONAL MATERIAL EXAMINED: *Paratypes:* MEXICO: Hidalgo, 4 km NE of Tlanchinol on Hwy. 105, 98°39′W, 21°02′N, ca. 1371 m. Cloud forest edge. 14.vi.1983, W. Maddison, 1 female (MCZ 67463 in the same vial with the holotype). *Other material:* MEXICO: Veracruz, 12 km S of Yecuatla on Hwy. 127, near 96.8°W, 19.8°N, 1219 m. Cloud forest edge 83-077. 20.vi.1983, W. Maddison, 1 male (MCZ 67461).

Cyrtognatha orphana, new species
Figures 22, 23

TYPE: Male holotype from Brazil, São Paulo olov., Cuv-Cucho [*sic*] (MNHN 9192). The label does not provide collector or date information. The label in the vial had the handwritten name "*Cyrtognatha fusciceps*". Most probably it was chosen by its original collector, but unfortunately he/she did not describe the species. The author of this name remains unknown, and thus we chose a different species name to describe this species.

ETYMOLOGY: The species epithet is an adjective taken from the Latin word for *orphan*, in reference to the lost identity of the arachnologist that first realized that these specimens belonged to an undescribed species of *Cyrtognatha*.

DIAGNOSIS: This species can be distinguished easily from all other *Cyrtognatha* species by the conspicuously prolaterally slanted embolus (fig. 22A). It differs significantly from similar congeners (namely, *C. insolita* and *C. petila*) in that both *C. insolita* and *C. petila* have the embolus with an extensive membrane that carries small outgrowths (serrated membrane) and have a triangular metine embolic apophysis (fig. 22A, C). The basal apophysis of the conductor in *C. orphana* has a well-developed membranous lamina (fig. 22C), while in *C. insolita* it has a sharpened tip (fig. 37C). In *C. petila* the membrane of the basal apophysis of the conductor is much smaller and the tip is sharpened as in *C. insolita*.

DESCRIPTION: *Male* (*holotype*). Habitus as in figure 23A–D. Carapace yellowish with brownish cephalic region. Fovea well marked with darker pigmentation. Abdomen cylindrical with small proximal tubercle. Distal tubercle short and extending over the spinnerets. Abdomen yellowish with numerous guanine spots concentrated dorsolaterally; dorsally and ventrally the guanine patches are absent around its longitudinal axis. Legs yellowish with remains of greenish coloration. Total length 6.02. Cephalothorax 2.32 long, 1.50 wide, 1.00 high. Abdomen 3.70 long, 0.85 wide, 1.25 high. Sternum yellowish; 0.88 long, 0.78 wide. Endites darker with brown color. Clypeus height 1.3 times one AME diameter. AME larger than the rest of the eyes. ALE and PLE close to each other on short elevations. AME diameter 0.15. Distance between AME slightly more than their diameter; AME–ALE distance 1.5 times one AME diameter. AME–PME distance at about one AME diameter. Distance between PME equal to their diameter. Chelicerae brown, very robust, and strongly divergent (fig. 23B). Cheliceral dorsal tooth very well developed, close to the fang articulation and conspicuously curved prolaterally. Femur I 5.14, 2.21 times the length of the cephalothorax. Pedipalp as in figure 22A–C. Palpal tibia length 0.25; cymbium length 0.95.

Female (*paratype*). Habitus and pigmentation pattern as in male. Carapace, chelicerae, and endites with lighter color than in male. Legs as in male with some remains of greenish coloring. Total length 6.41. Cephalothorax 2.25 long, 1.50 wide, 1.00 high. Abdomen 4.16 long, 1.22 wide, 1.22 high. Sternum 0.87 long, 0.87 wide. Chelicerae not divergent and without dorsal tooth; fang without outgrowth. Eyes as in male but AME closer to each other and to ALE. Distance between AME less than their diameter and between them and ALE equal to their diameter. AME diameter 0.12. Clypeus height 1.25 times one AME diameter. Femur I 4.65, 2.06 times the length of the cephalothorax. Vulva as in figure 22D, E.

DISTRIBUTION: This species is known only from the type locality (fig. 5).

ADDITIONAL MATERIAL EXAMINED: *Paratype:* BRAZIL: São Paulo olov., Cuv-Cucho, 1 female (MNHN 9192).

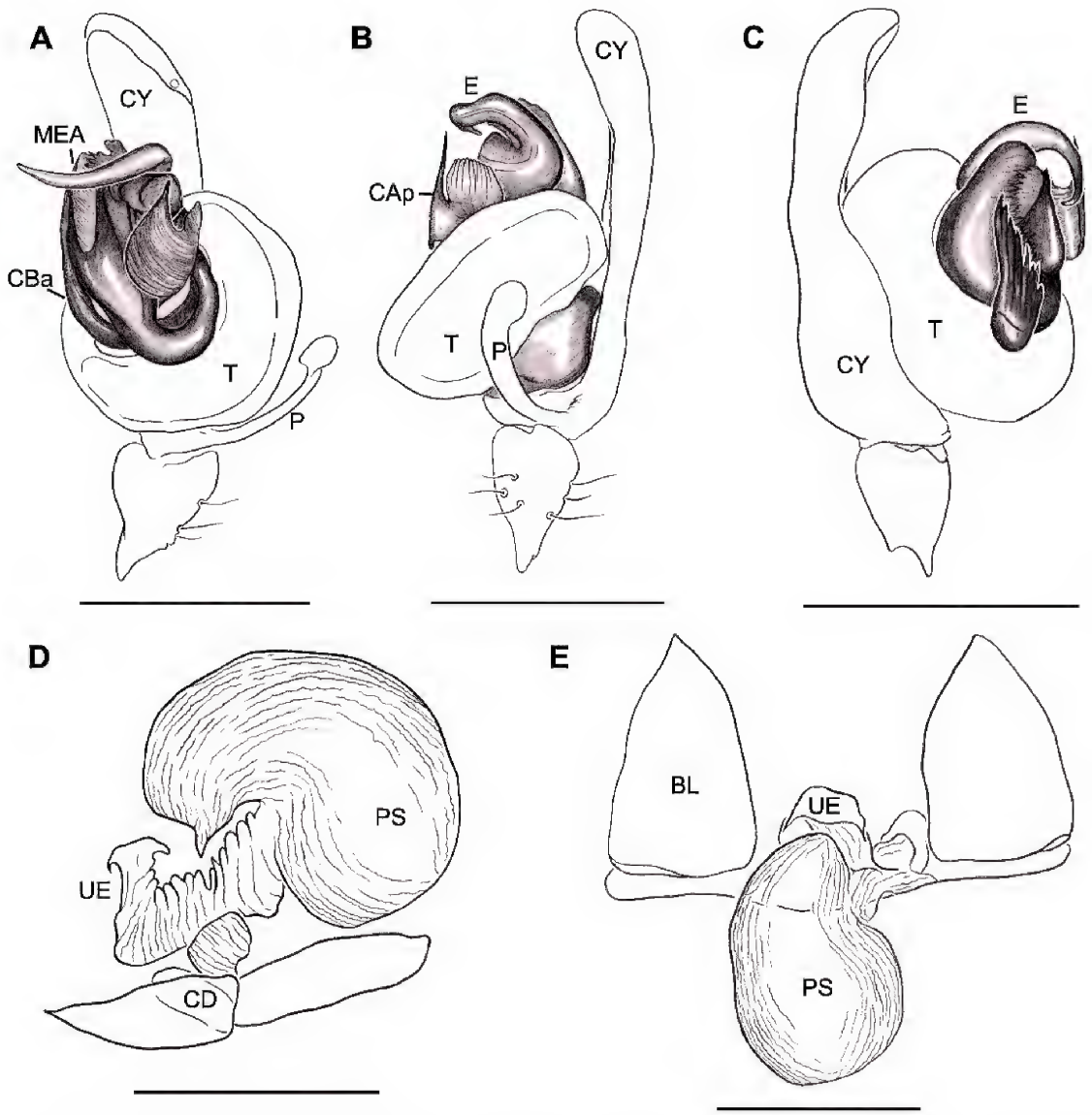

Fig. 22. *Cyrtognatha orphana*, n. sp. Male palp: (**A**), retrolateral (**B**), prolateral (**C**). Vulva: lateral (**D**), dorsal (**E**). Scale bars 0.5 mm.

Cyrtognatha pathetica, new species
Figure 24

TYPE: Female holotype from Guatemala. No date information on the label (BMNH 1890.7.1.5958).

Keyserling examined this specimen and named it "*C. sexmaculata*" (written on the label), but he never described this species.

ETYMOLOGY: The species epithet, a Latinized version of the Greek word *pathetikos*, is an adjective that refers to the pitiful physical condition of the only known specimen of this species.

DIAGNOSIS: *Cyrtognatha pathetica* can be easily distinguished from the similar *C. paradoxa* and *C. lepida* by the shape of the copulatory ducts that, in *pathetica*, are cylindrical and distally narrow (fig. 24B). *C. pathetica* does not have the chitinized ridge on the basal chamber present in *C. paradoxa* and *C. lepida*.

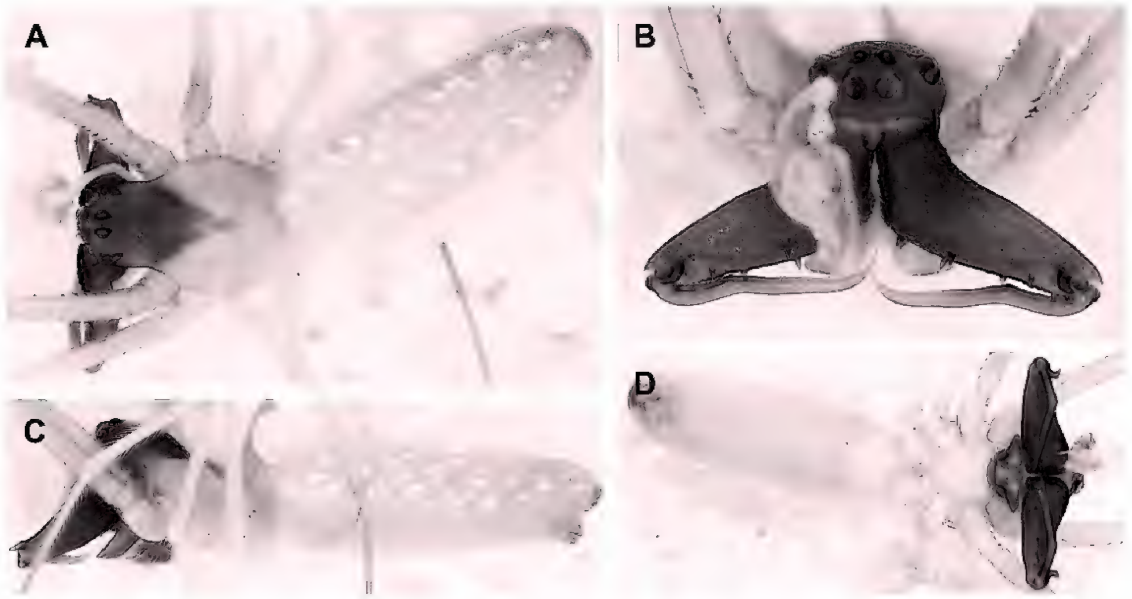

Fig. 23. *Cyrtognatha orphana*, n. sp. Male habitus: dorsal (**A**), lateral (**C**), ventral (**D**). Male chelicerae (**B**).

DESCRIPTION: *Male*. Unknown.

Female (*holotype*). Habitus as in figure 24F–H. Carapace with light brownish coloring, slightly darker in the center. Fovea well marked. Abdomen cylindrical with gray-brownish color and strongly reduced proximal and distal tubercles. Spinnerets brownish, darker than the rest of the abdomen. Some remains of the guanine patches still can be observed. Legs long, darker than the cephalothorax. Total length 6.82. Cephalothorax 1.86 long, 1.24 wide, 0.93 high. Abdomen 4.96 long, 1.24 wide, 1.30 high. Sternum yellowish; 0.99 long, 0.86 wide. Endites and labium darker with brown pigmentation. Clypeus height 0.8 time one AME diameter. All eyes surrounded by darker pigmentation. ALE and PLE a bit smaller than the other eyes and placed very close to each other on short elevations. AME diameter 0.12. Distance between AME slightly less than their diameter; AME–ALE distance at about two AME diameters. Distance between PLE equal to their diameter. Chelicerae yellowish, not divergent and without dorsal tooth. Femur I 4.34, 2.3 times the length of the cephalothorax. Vulva as in figure 24A–C, E. Epigastric furrow as in figure 24E.

DISTRIBUTION: The type locality is not actually specified on the label. The only information regarding the distribution of this species available at present is that it was collected somewhere in Guatemala (fig. 5).

Cyrtognatha pachygnathoides (O. P.-Cambridge, 1894) Figures 25–30

Tetragnatha pachygnathoides O. P.-Cambridge, 1894: 144, pl. 18, fig. 4.

Agriognatha pachygnathoides O. P.-Cambridge, 1896: 213.

Cyrtognatha pachygnathoides Petrunkevitch, 1911: 335.

TYPE: Male holotype, no collector or locality data (BMNH 1905.11.25.2228; examined). In the original description O. P.-Cambridge suggested that the specimen was collected in Chiriqui, Panama.

DIAGNOSIS: This species is very similar to the closely related *C. catia* but with a less pronounced curvature of the embolus. The most important diagnostic character separating these two species is the conspicuously widened distal part of the embolus in *C. pachygnathoides* (figs. 25B, C, 27C, I, J). The male chelicerae have a much smaller dorsal

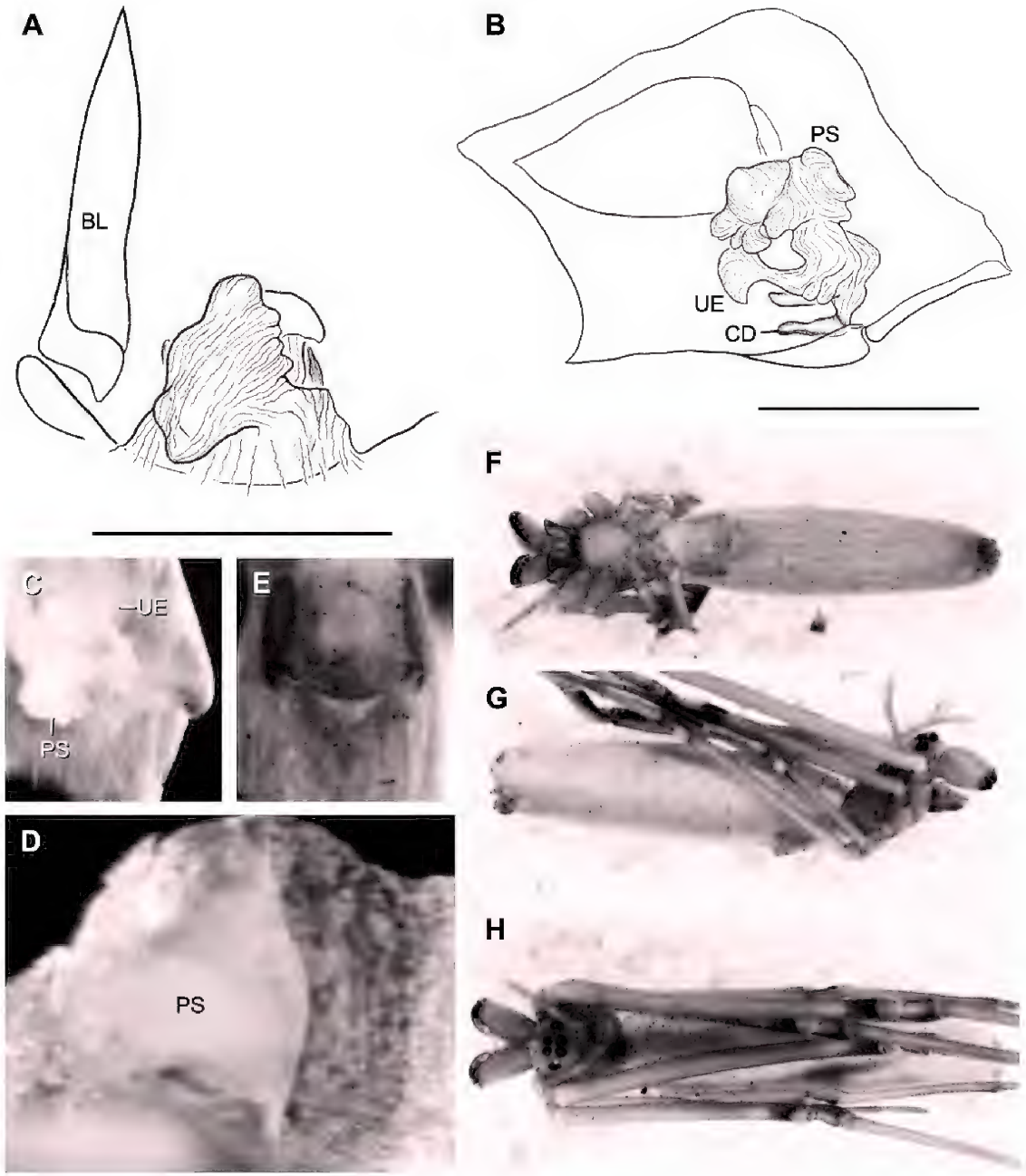

Fig. 24. *Cyrtognatha pathetica*, n. sp. Female vulva: dorsal (**A** and **D**), lateral (**B** and **C**). Female habitus: ventral (**F**), lateral (**G**), dorsal (**H**). Female epigastric furrow (**E**). Scale bars 0.5 mm.

tooth and strongly reduced outgrowths of the fangs (figs. 26B, 29A, C, E) than in *C. catia*.

DESCRIPTION: *Male* (*holotype*). Specimen in very poor condition. The abdomen and the chelicerae are missing. Most of the legs are disarticulated and the left palp and left legs I and II are lost. Carapace strongly depigmentated, yellowish, with a well-marked fovea. Sternum yellowish. Labium brownish but the endites lighter with yellowish color. Cephalothorax 2.02 long, 1.47 wide, 1.17 high. Sternum 1.02 long, 9.5 wide. Clypeus twice

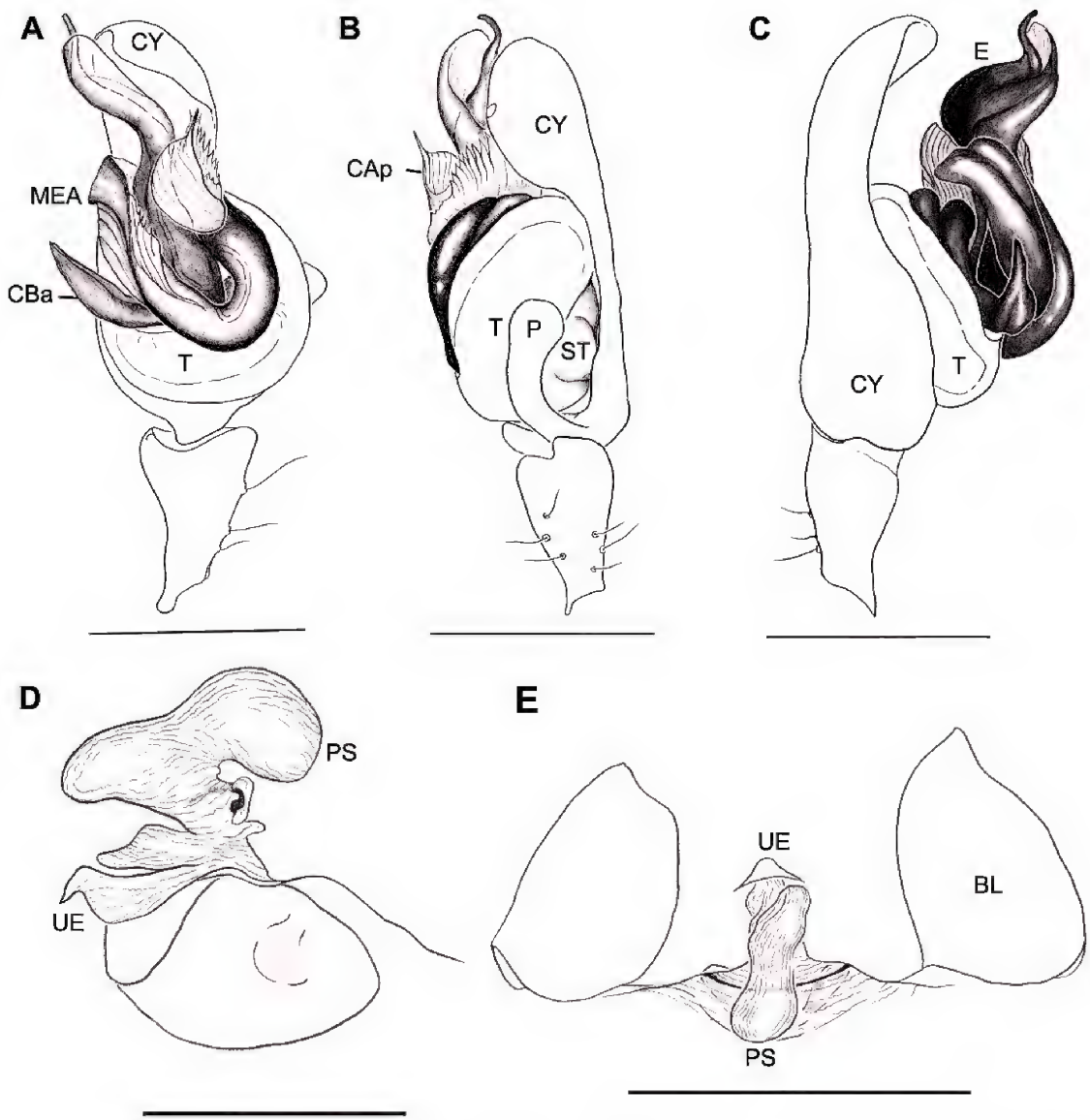

Fig. 25. *Cyrtognatha pachygnathoides*. Male palp: ventral (**A**), retrolateral (**B**), prolateral (**C**). Vulva: lateral (**D**), dorsal (**E**). Scale bars A–D: 0.5 mm; E: 1 mm.

one AME diameter. Eyes nearly the same size but PLE slightly smaller. AME diameter 0.10. Distance between AME equal to their diameter and between them and ALE twice their diameter. Distance between PLE equal to their diameter. The lateral eyes close together over well-developed elevations. Femur I 4.90, 2.4 times the length of the cephalothorax. Pedipalp as in figure 25A–C. Palpal tibia length 0.35; cymbium length 0.87.

Description of the specimen from El Volcán (Panama; 66543 MCZ). Habitus as in figure 26A–D. Carapace brownish with well-marked fovea (fig. 29C, D). Abdomen elongated with well-developed proximal and distal tubercles. Yellow-brownish with numerous reflecting guanine spots. Dorsally in the central part yellowish and without guanine spots. Total length 4.90. Cephalothorax 1.96 long, 1.47 wide, 0.98 high.

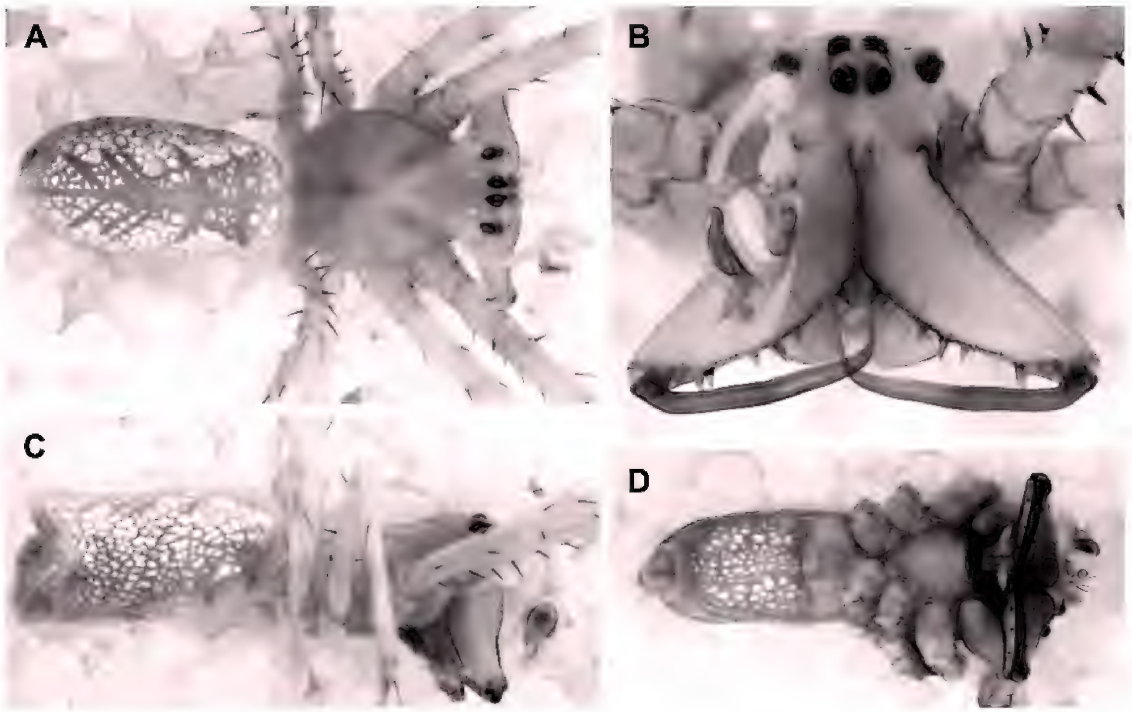

Fig. 26. *Cyrtognatha pachygnathoides*. Male habitus: dorsal (**A**), lateral (**C**), ventral (**D**). Male chelicerae (**B**).

Abdomen 2.94 long, 1.27 wide, 1.47 high. Sternum 1.07 long, 1.02 wide. Clypeus height 1.3 times one AME diameter. Eyes almost the same size except for the PLE, which are slightly smaller. AME diameter 0.14. The lateral eyes on well-pronounced elevations. The distance between the AME almost equal to their diameter. Distance between the PME equal to their diameter. AME–ALE distance twice one AME diameter; PLE–PME distance nearly twice the diameter of the PME. Chelicerae brownish, darker than the rest of the cephalothorax (figs. 26B, 29A, C, E). Dorsal cheliceral tooth very close to the fang articulation; with rounded tip and smaller than some of the other cheliceral teeth (fig. 29E). Femur I 4.90, 2.5 times the length of the cephalothorax. Pedipalp as in figures 25A–C, 27A–H. Palpal tibia length 0.34; cymbium length 0.88. Epiandrous fusules as in figure 27K. Male femur IV as in figure 29F.

Female (*paratype from the type locality*). Habitus and coloration as in male. Carapace with lighter tones. Female cephalothorax and abdomen as in figure 30A–D. Chelicerae not divergent and without dorsal tooth and fang outgrowth. Sternum yellowish with labium and endites lighter than in the male. Sternum 1.23 long, 1.22 wide. Abdomen with very well-developed proximal tubercles. The distal tubercle is very well developed, high, and with shape of thin cone. Total length 6.46. Cephalothorax 2.94 long, 2.00 wide, 1.56 high. Abdomen 3.52 long, 1.96 wide, 2.69 high. Eyes slightly smaller than in male. Lateral eyes on less pronounced elevations. Diameter of AME 0.14. Clypeus 1.17 times one AME diameter. Femur I 5.39, 1.83 times the length of the cephalothorax. Vulva as in figure 25D–E. Female genital opening as in figure 28I. Female spinnerets as in figure 28A–H, J.

Variation. Male cephalothorax ranges in length from 1.96 to 2.69 (n = 6). Female cephalothorax ranges in length from 2.94 to 3.81 (n = 9). Male total body length ranges from 4.90 to 5.87 (n = 6). Female total body length ranges from 6.46 to 8.71 (n = 9). The height of the distal tubercle is very variable, both in males and females. In males height of the distal tubercle varies from 1.47 to 1.70 (n = 6) and in females from 2.69 to 4.10 (n = 9).

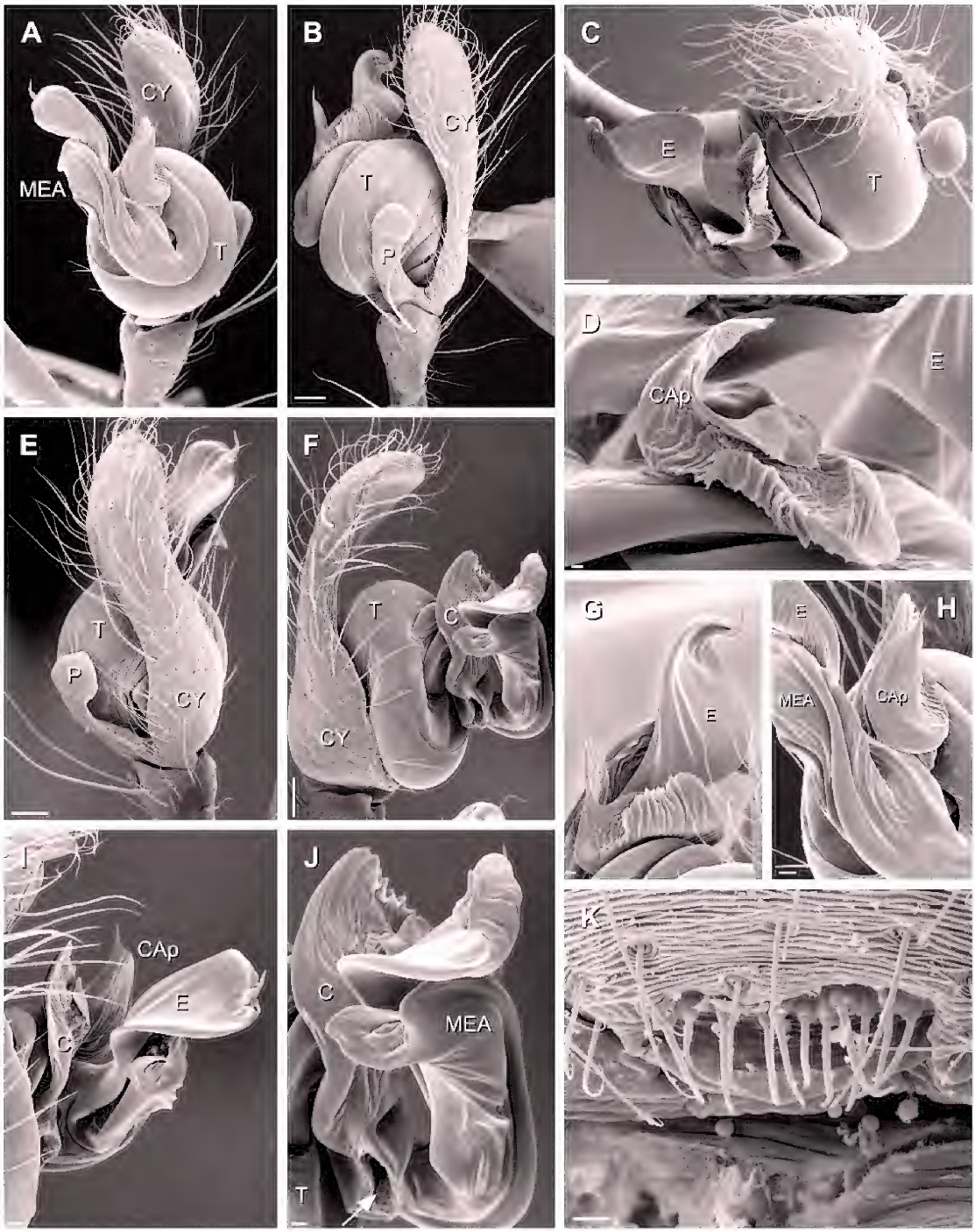

Fig. 27. *Cyrtognatha pachygnathoides*. Male palp: ventral (**A**), retrolateral (**B**), apical (**C**), dorsal (**E**), prolateral (**F**). Conductor: apical (**D**). Apical apophysis of the conductor and embolus dorsoretrolateral (**G**). Embolus and apical apophysis of the conductor ventral (**H**). Conductor and embolus prolateral (**I** and **J**) (arrow points to the base of the removed basal apophysis of the conductor). Epiandrous fusules (**K**). Scale bars A, B, C, E, F: 100 μm; I: 30 μm G, H, J: 20 μm; D, K: 10 μm.

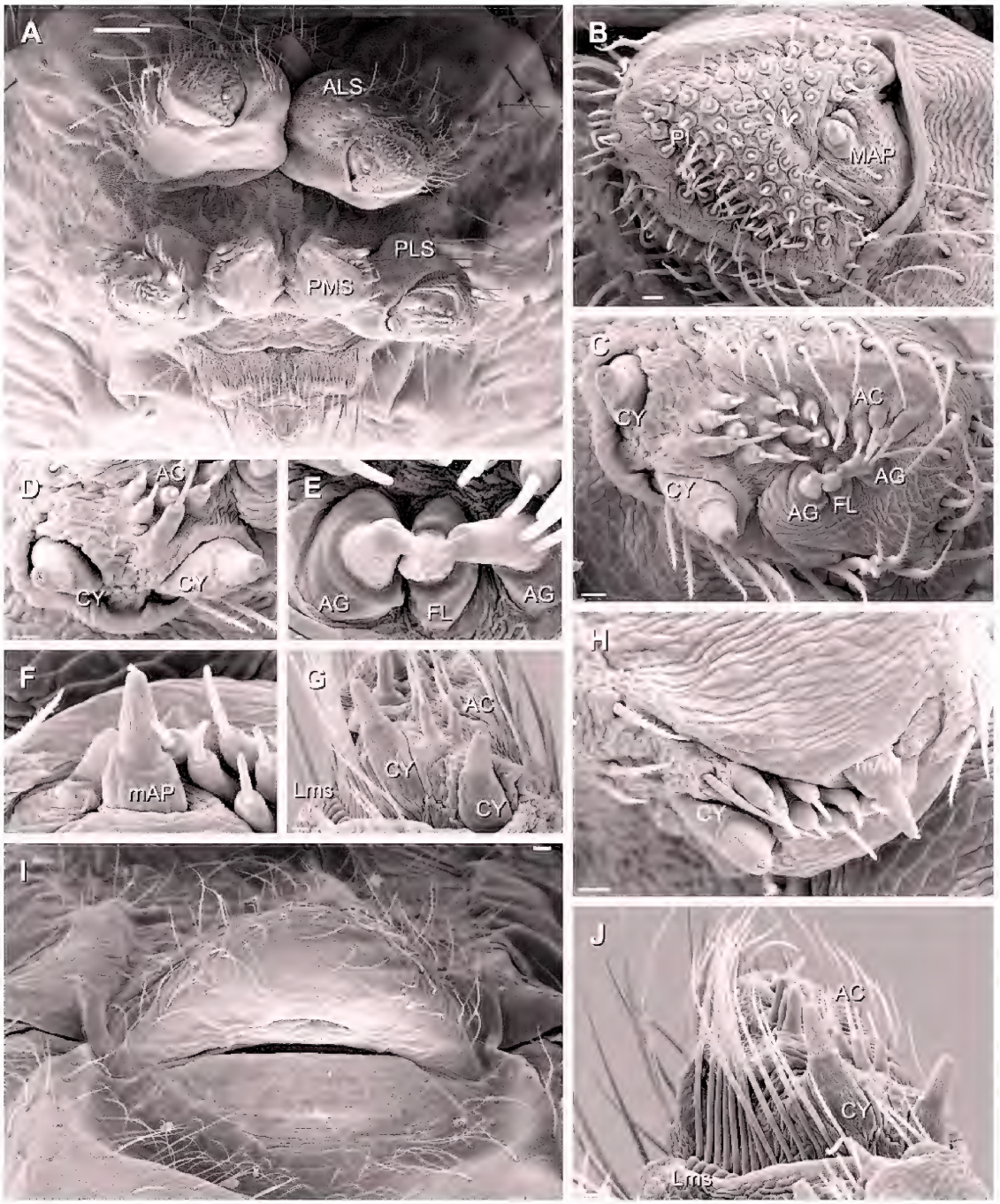

Fig. 28. *Cyrtognatha pachygnathoides*. Female spinnerets: ventral (**A**). Female ALS (**B**). Female PLS (**C–E, G, J**). Female PMS (**F** and **H**). Female genital opening ventral (**I**). Scale bars A: 100 μm; B–D, G, H, J: 10 μm; E: 1 μm; F: 2 μm; I: 30 μm.

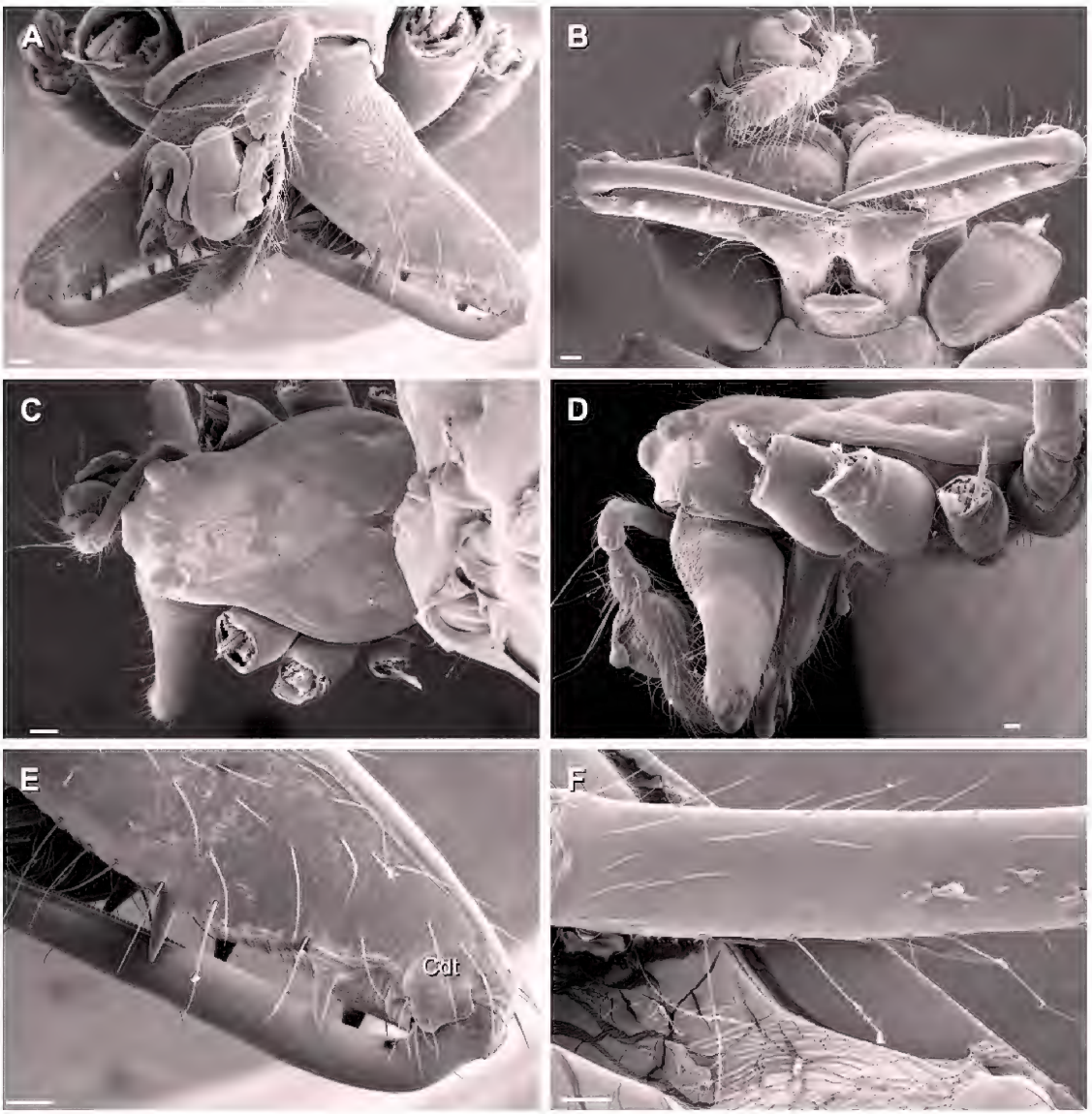

Fig. 29. *Cyrtognatha pachygnathoides*. Male chelicerae: frontal (**A** and **E**), ventral (**B**). Male cephalothorax: dorsal (**C**), lateral (**D**). Male femur IV: lateral (**F**). Scale bars 100 μm.

DISTRIBUTION: Costa Rica and Panama (fig. 5).

ADDITIONAL MATERIAL EXAMINED: PANAMA: Chiriquí, El Volcán. 26.ii.1936, W. J. Gertsch, 1 female (AMNH); Chiriquí, Cerro Punta. 4.iii.1936, W. J. Gertsch, 2 females (AMNH); El Volcán. viii.1950, A. M. Chickering, 1 m (MCZ 66543). COSTA RICA: Puntarenas, Area de Conservación La Amistad, Estación Pittier, 1800 m. 11.vi.1995, G. Hormiga, 1 male (USNM); Puntarenas, Area de Conservación La Amistad, Estación Pittier. 009°01′N, 82°5′W, 1820 m. 11.vi.1995, G. Hormiga, 1 male (USNM); Puntarenas, Area de Conservación La Amistad, Estación Pittier, 1750 m. 8–11.vi.1995, G. Hormiga, 2 males, 6 females (USNM, 1 male and 1 female used for SEM).

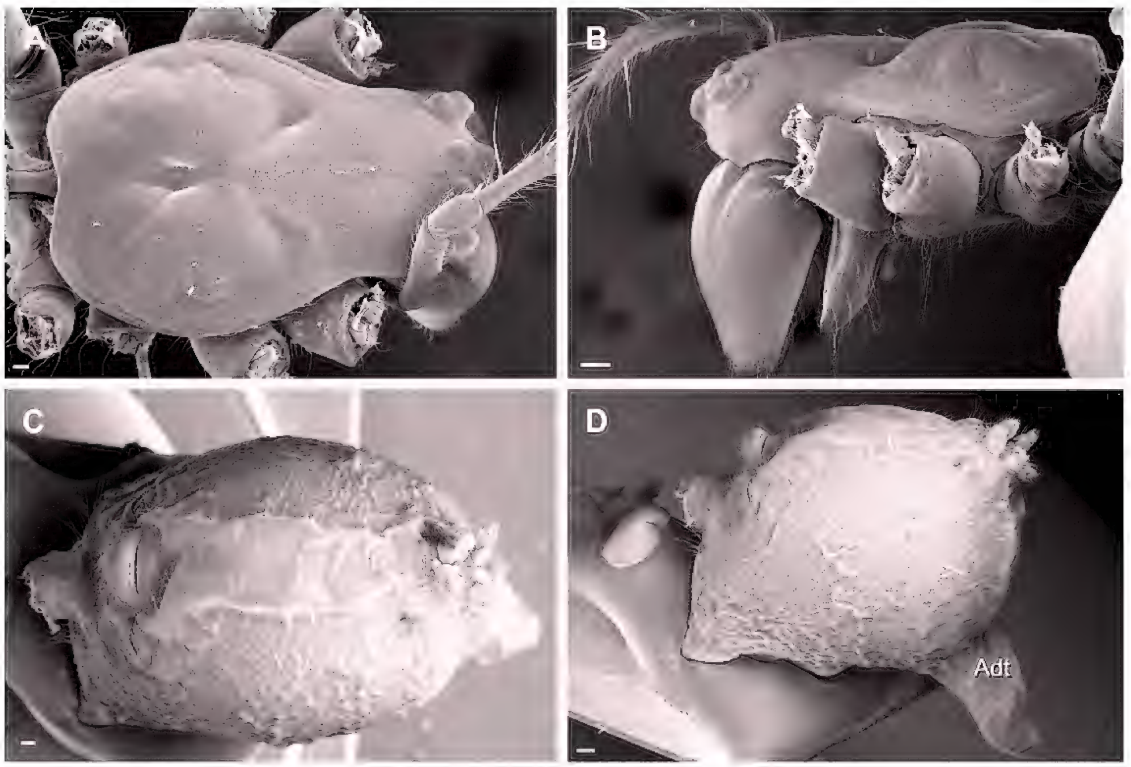

Fig. 30. *Cyrtognatha pachygnathoides*. Female cephalothorax: dorsal (**A**), lateral (**B**). Female abdomen: ventral (**C**), lateral (**D**). Scale bars A, D: 200 μm; B, C: 100 μm.

Cyrtognatha espanola (Bryant, 1945), new combination
Figures 31–36

Agriognatha espanola Bryant, 1945: 399, fig. 34.
Agriognatha espanola Dimitrov, Álvarez-Padilla & Hormiga, 2007: 761, figs. 3A–F, 10C–D, 12B.

TYPE: Male holotype from Haiti, Kensk-off, 1310 m, 1.v.1935, Roys (the only reference on the label, which might refer to the collector) (MCZ 21226; examined).

DIAGNOSIS: This species shares numerous similarities with *C. rucilla* and *C. simoni*, and its correct identification can be difficult. To distinguish the males of these species the most important character is the shape of the tip of the embolus. In ventral view in *C. espanola* the embolus tip is curved prolaterally (fig. 31A), in *C. rucilla* it is curved retrolaterally (fig. 41A), and in *C. simoni* it is almost straight (fig. 47A). The shape of the embolus in prolateral view is also very useful for identification. In *C. espanola* it is arched and the tip of the embolus is additionally curved at almost 90° (fig. 31C); in *C. rucilla* the embolus is nearly straight and the tip of the embolus is S-shaped (fig. 41A–C); in *C. simoni* the embolus is almost straight but the tip of the embolus is curved at 90° as in *C. espanola* (fig. 47A–C). The shape of the male chelicerae is also diagnostic for these three species. In *C. espanola* the male chelicerae are widely divergent and very robust (figs. 32B, 35A, B, D); *C. rucilla* has also very robust chelicerae but they are less divergent that in *C. espanola* and *C. simoni*; *C. simoni* has strongly divergent chelicerae but they are much thinner than in the other two species. The females of *C. espanola* can be easily distinguished from closely related species by the size and shape of the sacs in the vulva (fig. 31D, E).

DESCRIPTION: *Male* (*holotype*). Habitus as in figure 32A–D. Carapace brown-yellowish with a well-marked fovea and darker band medially. Abdomen cylindrical, brown-grayish, guanine almost missing (in paratypes guanine spots concentrated dorsolaterally).

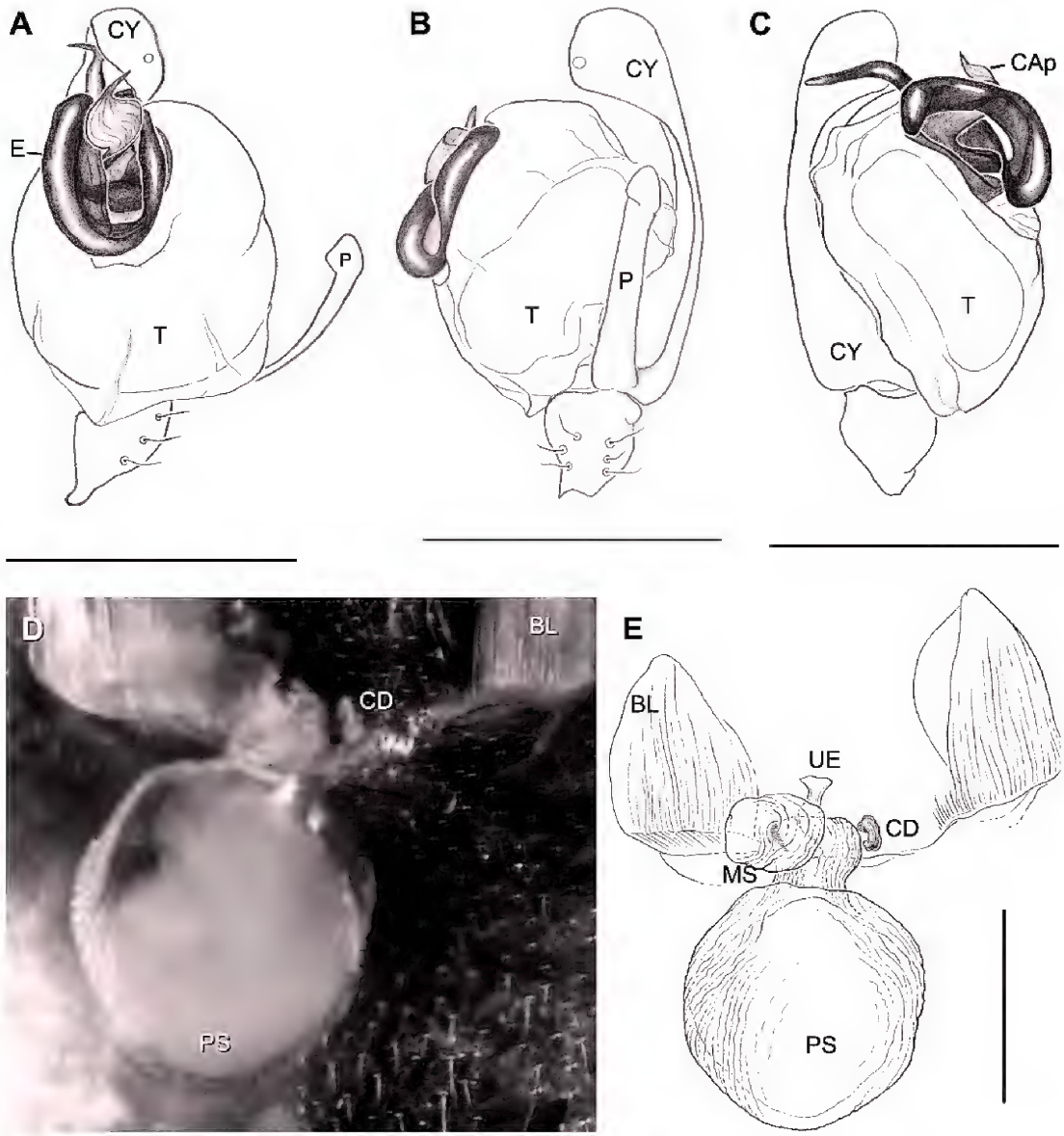

Fig. 31. *Cyrtognatha espanola*. Male palp: ventral (**A**), retrolateral (**B**), prolateral (**C**). Female vulva: dorsal (**D** and **E**). Scale bars 0.5 mm.

Dorsal tubercles strongly reduced. Dorsally two longitudinal lines, each with four dark brown spots, are present distally. Total length 4.06. Cephalothorax 1.56 long, 1.20 wide, 0.5 high. Abdomen 2.50 long, 1.12 wide, 1.12 high. Sternum yellowish with darker margins; 0.85 long, 0.75 wide. Clypeus height 1.2 times one AME diameter. AME diameter 0.09. All eyes nearly the same size and surrounded with darker pigmentation. Distance between AME equal to their diameter; between them and ALE 2.5 AME diameters; distance to PLE 1.5 AME diameters. Distance between PLE equal to their diameter. Chelicerae (figs. 32B, 35A, B, D) dark brown, moderately divergent with a well-developed dorsal tooth. Dorsal tooth with very wide base and close to the fang joint. The rest of the cheliceral teeth well developed. Cheliceral fang with very small

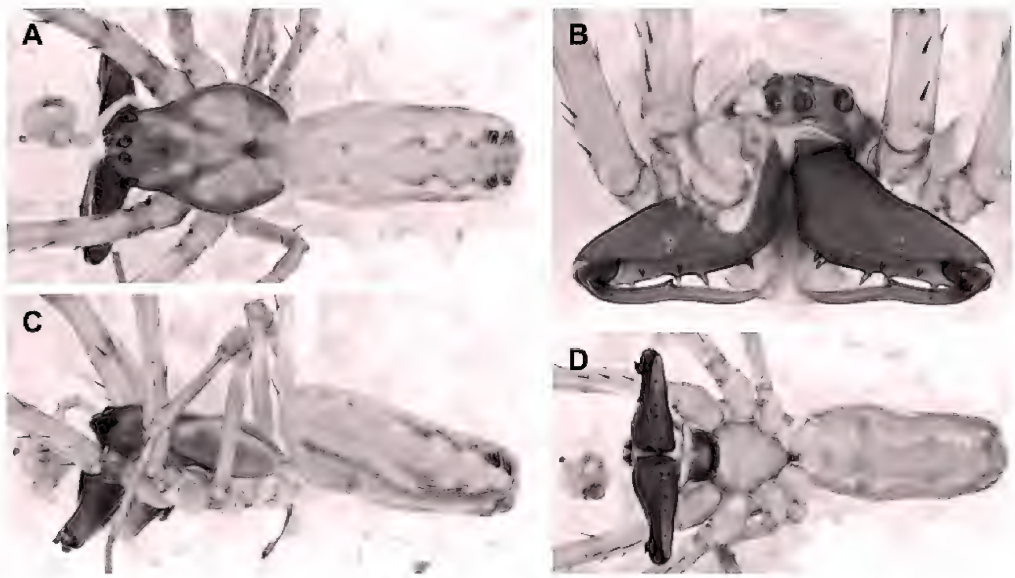

Fig. 32. *Cyrtognatha espanola*. Male habitus: dorsal (**A**), lateral (**C**), ventral (**D**). Male chelicerae (**B**).

outgrowth (fig. 35D) and almost straight except for its apical end. Femur I 3.72, 2.3 times the longitude of the cephalothorax. Pedipalp as in figures 31A–C, 33A–H, 34A. Palpal tibia length 0.13; cymbium length 0.62. Male epiandrous fusules as in figure 34F.

Female (*paratype from the type locality*). Habitus and coloration as in male. Abdomen with large distal tubercle, which in this species is placed almost in the center of the abdomen. As in the male, the type specimen almost without guanine (but present in paratypes). Chelicerae not divergent and without dorsal tooth. Total length 4.95. Cephalothorax 1.85 long, 1.25 wide, 1.00 high. Abdomen 3.10 long, 1.86 wide, 2.17 high. Sternum 0.62 long, 0.57 wide. Clypeus half of an AME diameter. AME diameter 0.08. Femur I 2.85, 1.5 times the length of the cephalothorax. Vulva as in figures 31D, E, 34B–E. Spinnerets as in figures 35C, E–H, 36A. Female cephalothorax and abdomen as in figure 36C–F. Female femur IV as in figure 36B.

Variation. Male cephalothorax length varieis between 1.47 and 1.96 (n = 26). Females cephalothorax length varies between 1.85 and 1.96 (n = 31). Total body length in males varies between 3.18 and 4.26 (n = 26) and in females between 4.95 and 6.02 (n = 31). The size and placement of the distal dorsal tubercle in females varies. In some specimens the tubercle is placed in the distal third of the abdomen, while in others it is located almost in the middle.

DISTRIBUTION: This species is widely distributed over the higher zone of Hispaniola (fig. 5).

ADDITIONAL MATERIAL EXAMINED: *Paratypes:* HAITI: Kenskoff, 1310 m. 1.v.1935, Roys, 1 female (*allotype*, MCZ 44013); Kenskoff, 914–1219 m. 1.v.1935, Roys 1 male, 2 females (MCZ 66548); Dame-Marie, 1941, A. Audant, 1 male (MCZ 66549). DOMINICAN REPUBLIC: 914–1219 m. vii.1938, P.J. Darlington, 1 female (MCZ 66551). *Other material*: HAITI: 25 mi. from Aux Cayes, 29.viii.1935, W.G. Hassler, 2 males, 5 females (NMHN). DOMINICAN REPUBLIC: Barahona Prov., Paraíso, Reserva Natural Cachote, cloud forest and secondary growth. 18°05′54.8″N, 71°11′22.0″W, 1220 m, 6–9.IV.2005, G. Hormiga, F. Álvarez, and S. Benjamín, 27 females, 16 males (MCZ); La Vega Prov., Constanza, Reserva Científica Ébano Verde, Casa Vito, 19°01′47.8″N, 70°30′56.5″W, 1400 m, 15.IV. 2005, F. Álvarez and S. Benjamin, 7 males (MCZ).

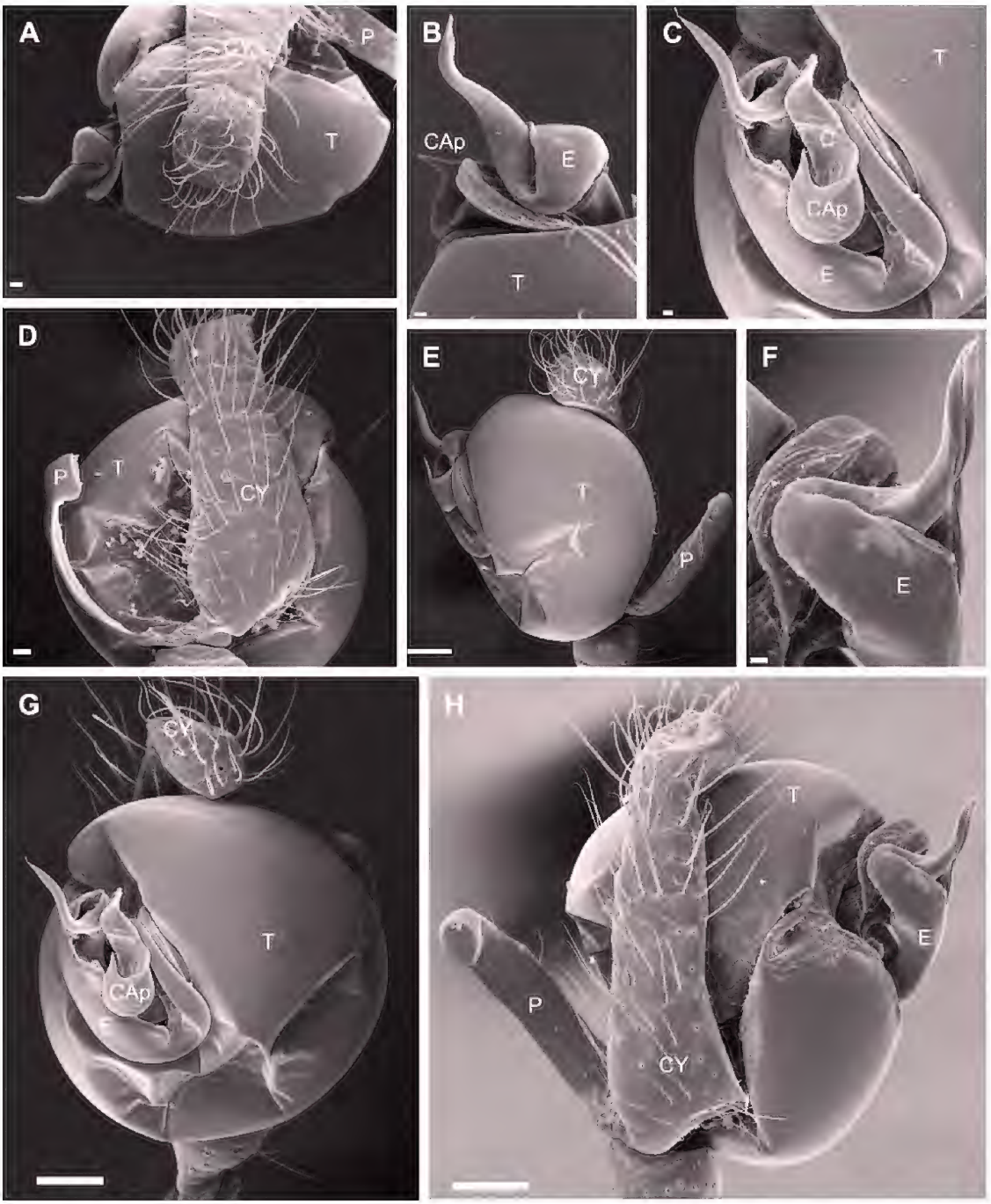

Fig. 33. *Cyrtognatha espanola*. Male palp: apical (**A**), dorsal (**D**), retrolateral (**E**), ventral (**G**), dorsoprolateral (**H**). Embolus tip (**B** and **F**). Embolus ventral (**C**). Scale bars A: 20 μm; B, C, F: 10 μm; D: 30 μm; E, G, H: 100 μm.

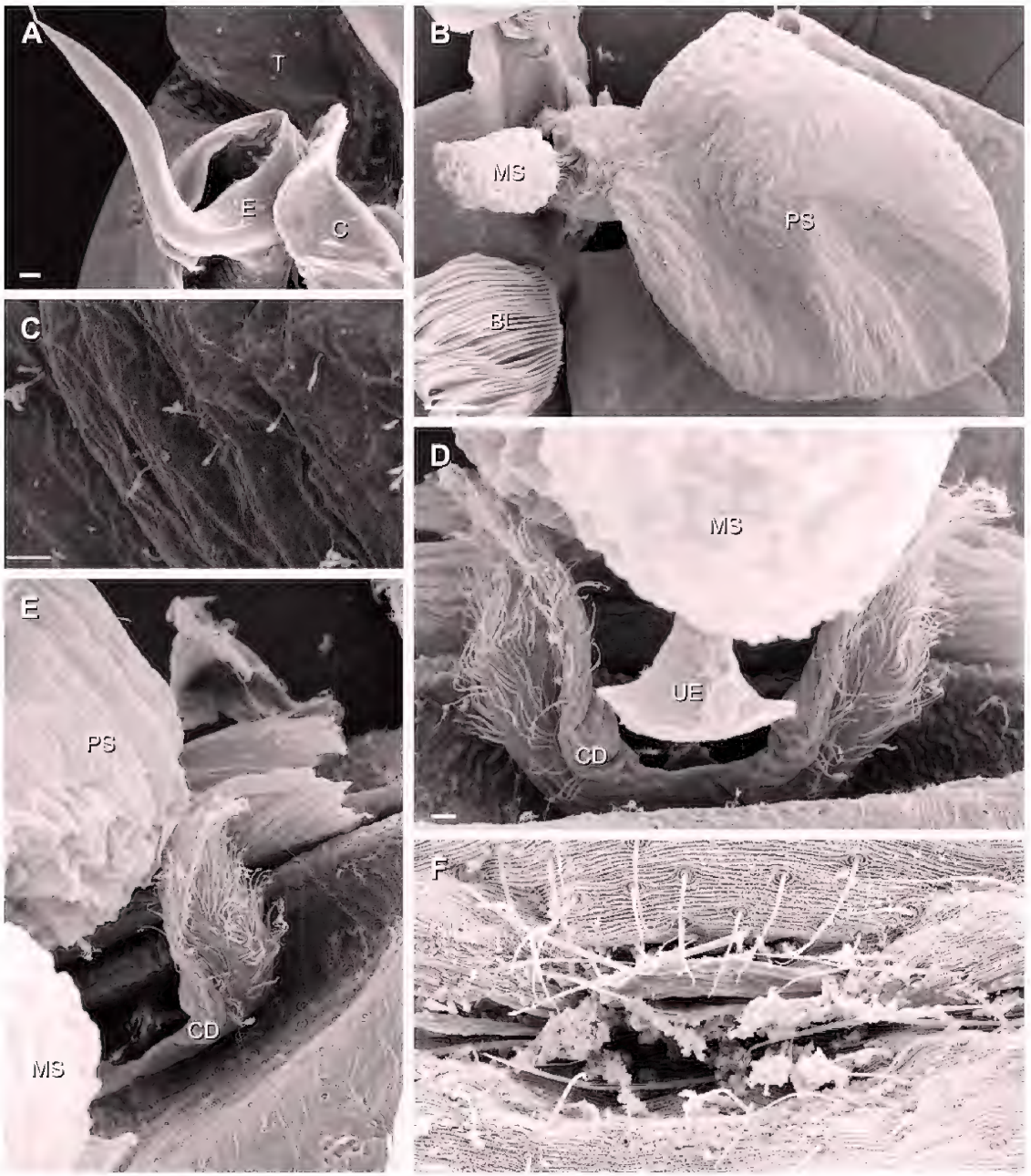

Fig. 34. *Cyrtognatha espanola*. Embolus tip (**A**). Female vulva: dorsal (**B**) (Dimitrov et al., 2007: fig. 3A). Cuticle with short stem ductules of the posterior sac (**C**) (Dimitrov et al., 2007: fig. 3B). Uterus externus and copulatory ducts: frontal (**D**) (Dimitrov et al., 2007: fig. 3F). Copulatory ducts: lateral (**E**). Epiandrous fusules (**F**). Scale bars A, C–F: 10 μm; B: 100 μm.

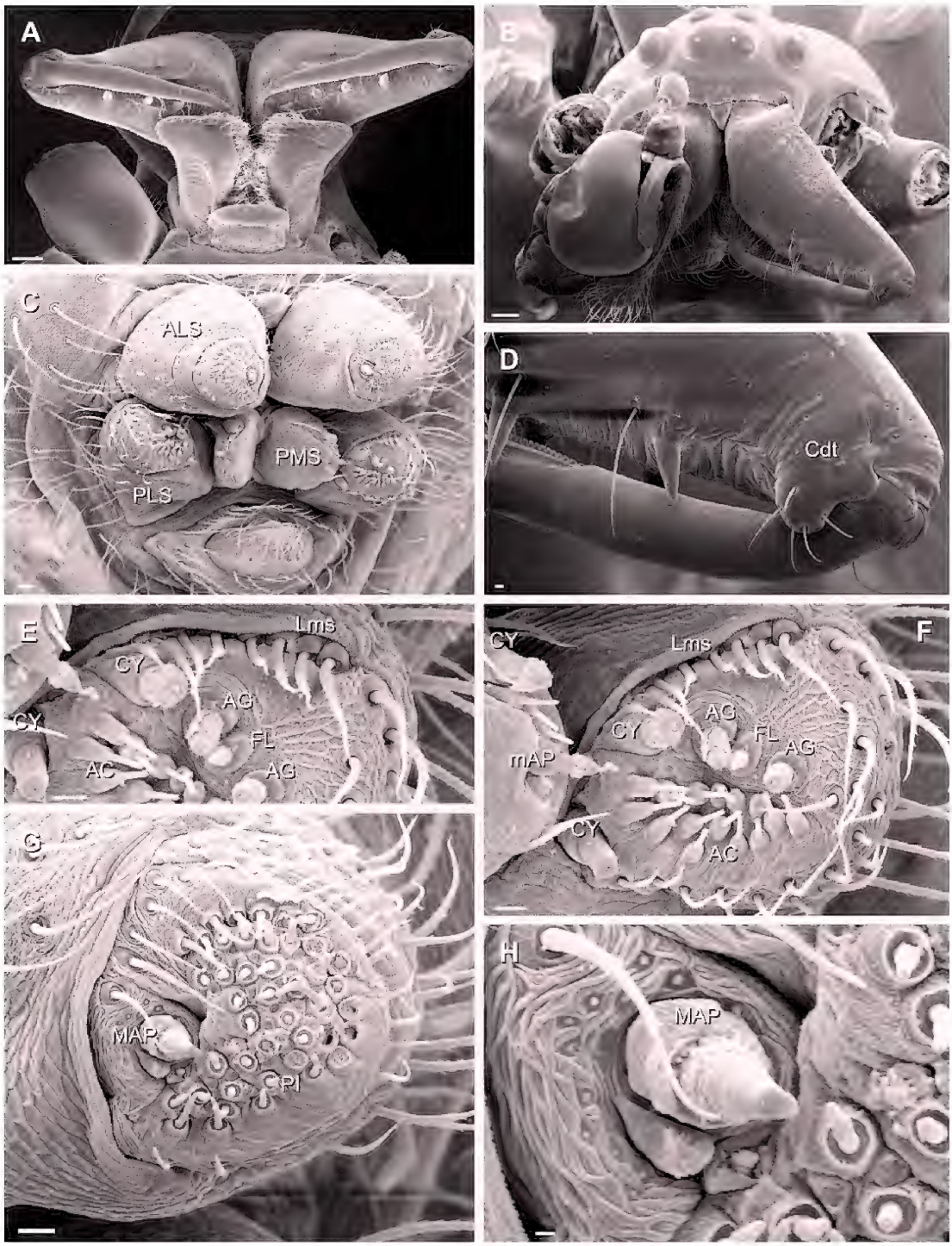

Fig. 35. *Cyrtognatha espanola*. Male chelicerae: ventral (**A**), frontal (**B**), cheliceral dorsal tooth (**D**). Female spinnerets: ventral (**C**), PLS (**E** and **F**), ALS (**G** and **H**). Scale bars A, B: 100 μm; C: 20 μm; D–G: 10 μm; E: 3 μm; H: 2 μm.

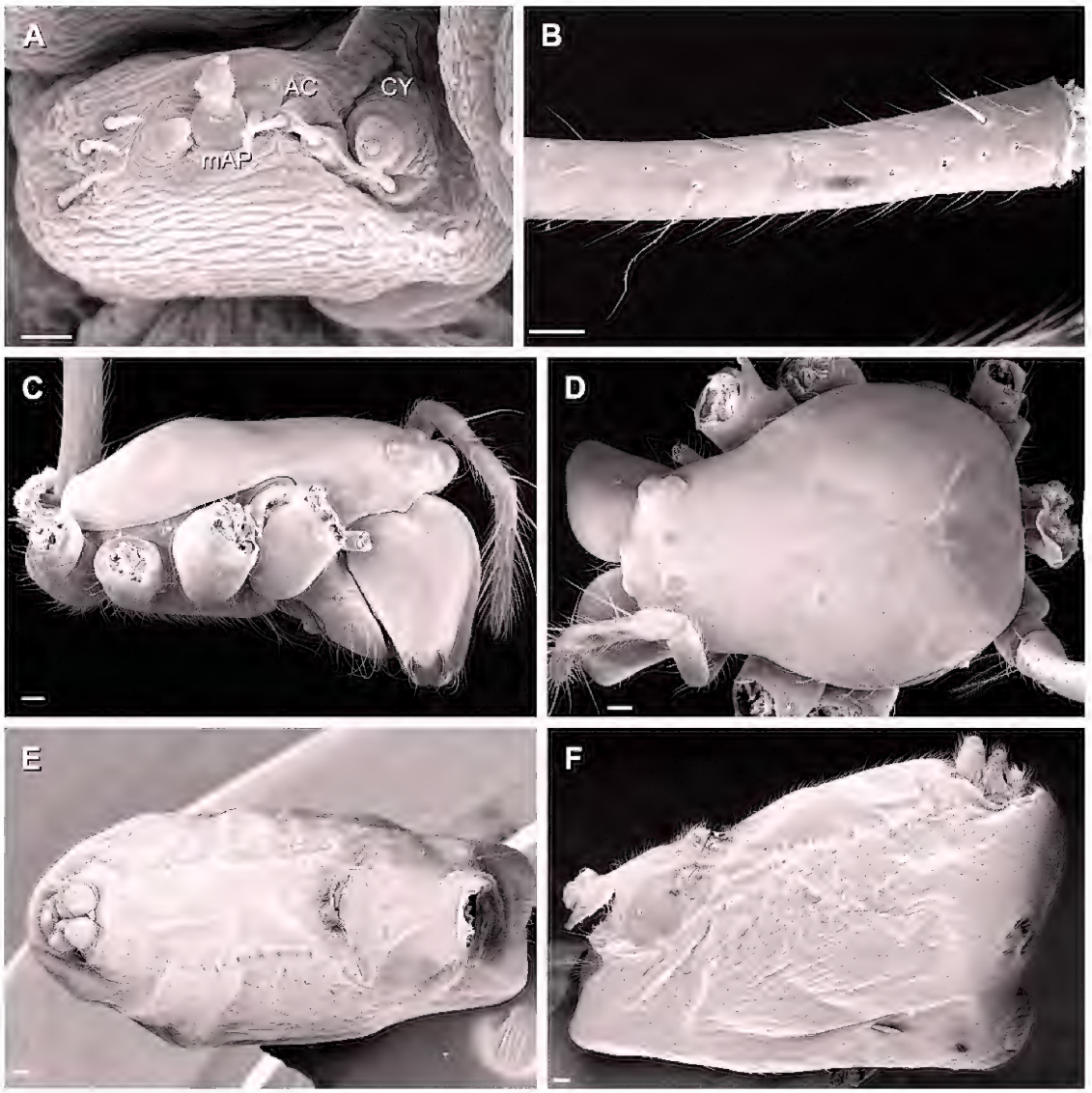

Fig. 36. *Cyrtognatha espanola*. Female PMS (**A**). Female leg IV femur (**B**). Female cephalothorax: lateral (**C**), dorsal (**D**). Female abdomen: ventral (**E**), lateral (**F**). Scale bars A: 10 μm; B–F: 100 μm.

Cyrtognatha insolita (Chickering, 1956), new combination
Figures 37–40

Agriognatha insolita Chickering, 1956b: 2, figs. 1–6.
Agriognatha insolita Dimitrov, Álvarez-Padilla & Hormiga, 2007: 763, figs. 5A–F, 10–B.

TYPE: Male holotype from Panama, Barro Colorado Island, Canal Zone. viii.1950, A. M. Chickering (MCZ 21668; examined).

DIAGNOSIS: This species can be easily distinguished from other congeners with triangular metine embolic apophysis by the presence of a very characteristic serrated membrane covering a large area of the embolus ventrally and part of the base of the metine embolic apophysis (figs. 37A, C, 39I, J). The shape of the apical apophysis of the conductor and the morphology of the paracymbium are also diagnostic. Another important diagnostic character, which in most of the cases can be enough by itself to identify this species, is the shape of the dorsal cheliceral tooth (fig. 38B, E, F, H). In *C.*

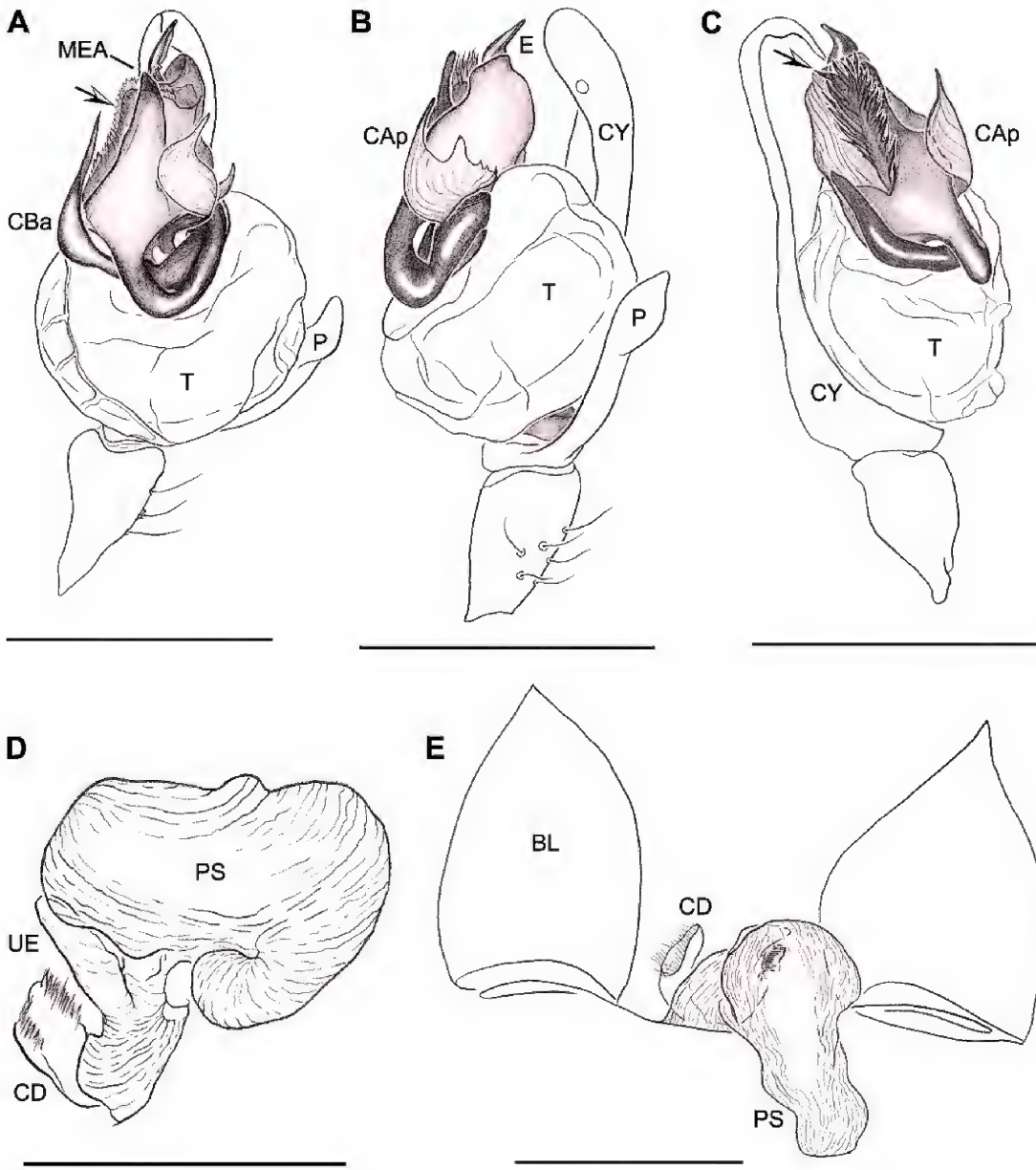

Fig. 37. *Cyrtognatha insolita*. Male palp: ventral (**A**), retrolateral (**B**), prolateral (**C**). Vulva: lateral (**D**), dorsal (**E**). Scale bars A–E 0.5 mm. Arrow points to the embolic serrated membrane.

insolita species its tip is conspicuously bifurcated and both parts are sharpened, while in all similar species (*C. orphana* and *C. petila*) the dorsal cheliceral tooth never has two sharpened edges. Female diagnostic characters include the shape of the copulation ducts (fig. 37D, E) and the shape of the membranous sac (posterior sac) holding the sperm, which is elongated (fig. 37D, E). Additionally, in *C. insolita* the median sac is reduced to a short cylindrical structure.

DESCRIPTION: *Male* (*holotype*). Habitus as in figure 38A–D. Carapace yellow-brownish; darker anteriorly with a well-marked fovea. Abdomen cylindrical, yellowish with few remains from the guanine spots. Dorsal

Fig. 38. *Cyrtognatha insolita*. Male habitus: dorsal (**A**), ventral (**C**), lateral (**D**). Male chelicerae: frontal (**B** and **F**), ventral (**H**). Cheliceral dorsal tooth (**E**). Epiandrous fusules (**G**). Scale bars E: 20 μm; F, H: 100 μm; G: 10 μm.

tubercle small. Total length 5.58. Cephalothorax 2.17 long, 1.42 wide, 1.16 high. Abdomen 3.41 long, 0.93 wide, 0.93 high. Sternum yellowish, 0.93 long, 0.87 wide. Chelicerae strongly divergent with dark brown color. Dorsal tooth very well developed, outlying the fang joint and with bifurcated tip. The prolateral division of the dorsal tooth sharp and curved, while the retrolateral division is fairly blunt and carries

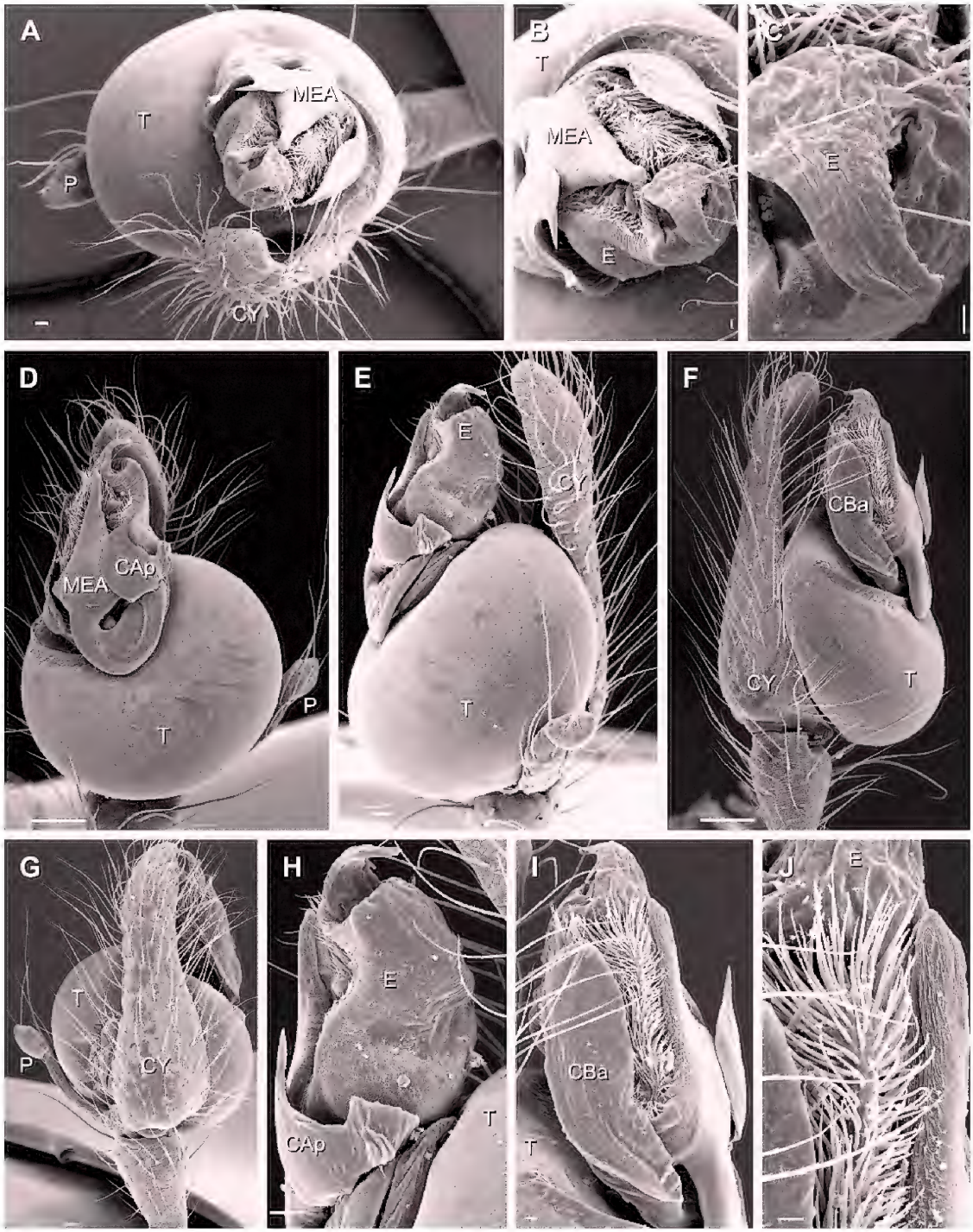

Fig. 39. *Cyrtognatha insolita*. Male palp: apical (**A**), ventral (**D**), retrolateral (**E**), prolateral (**F**), dorsal (**G**). Embolus and conductor: apical (**B**). Embolus tip: apical (**C**). Embolus and conductor: retrolateral (**H**). Embolus and conductor prolateral (**I**). Serrated membrane of the embolus (**J**). Scale bars A: 20 μm; B, C, I, J: 10 μm; D, F: 100 μm; E, G, H: 30 μm.

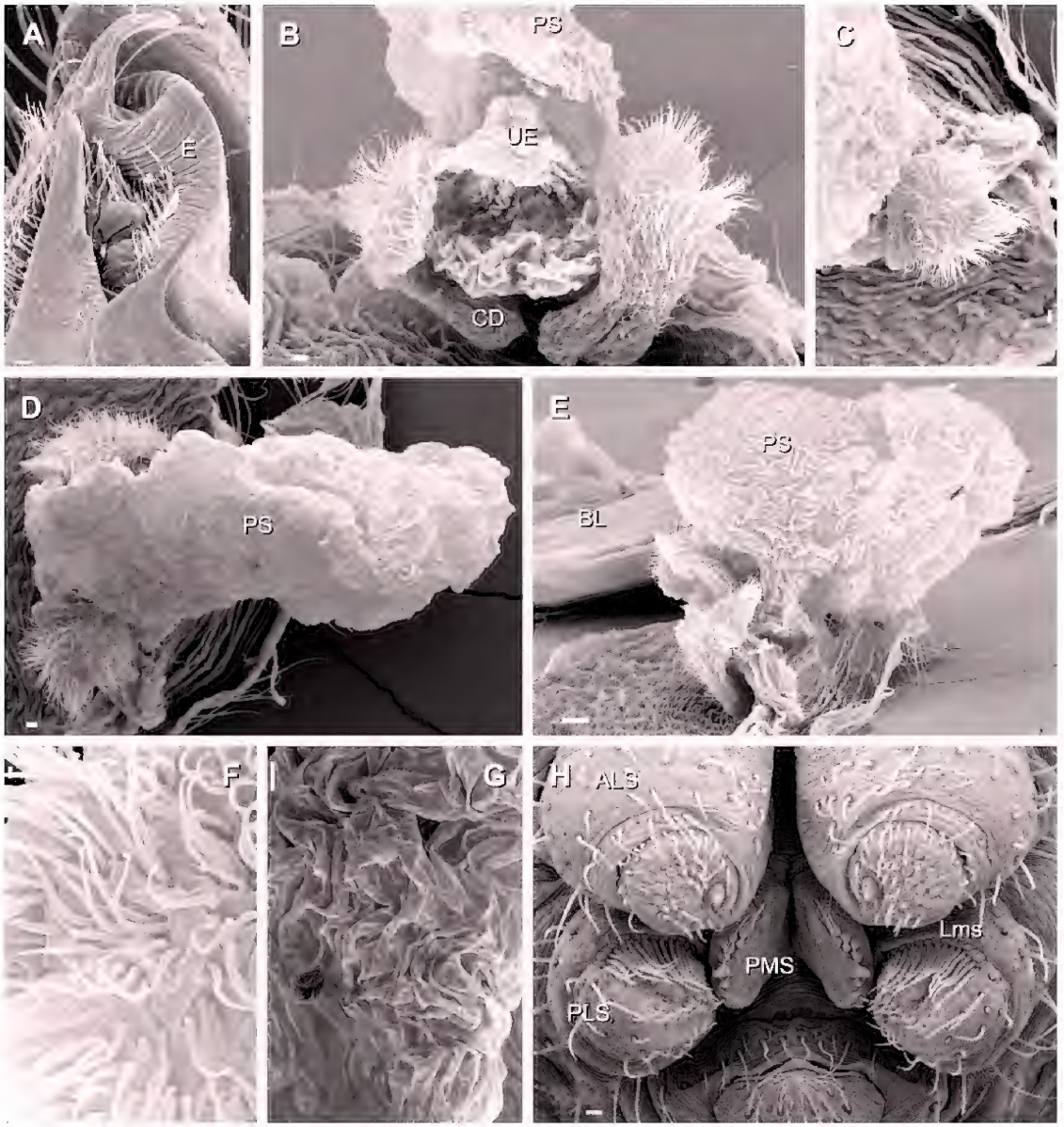

Fig. 40. *Cyrtognatha insolita*. Embolus tip: ventral (**A**). Vulva: frontal (**B**) (Dimitrov et al., 2007: fig. 5F). Copulatory duct tip (**C**) (Dimitrov et al., 2007: fig. 5E). Vulva: dorsal (**D**) (Dimitrov et al., 2007: fig. 5A). Vulva: lateral (**E**) (fig. 5C of Dimitrov et al., 2007). Long ductule glands (**F**) (fig. 5D of Dimitrov et al., 2007). PS cuticle (**G**) (fig. 5B of Dimitrov et al., 2007). Male spinnerets (**H**). Scale bars A–C, G, H: 10 μm; D: 20 μm; E: 30 μm; F: 2 μm.

several setae. Chelicerae as in figure 38B, E, F, H. Clypeus height 1.25 times one AME diameter. AME diameter 0.15. AME slightly larger than the rest of the eyes. Distance between AME equal to their diameter; between them and ALE 1.5 times one AME diameter; AME–PME distance one AME diameter. Distance between PME half of their diameter. PLE smaller than the ALE. Femur I 4.03, 1.8 times the length of the cephalothorax. Pedipalp as in figures 37A–C, 39A–J, 40A. Palpal tibia length 0.27; cymbium length 0.75. Epiandrous fusules as in figure 38G. Spinnerets as in figure 40H.

Female (*paratype from the type locality*). Habitus and coloration as in male except for the lighter carapace. Chelicerae not divergent, without dorsal tooth and lighter in color. Total length 8.12. Cephalothorax 2.79 long, 1.73 wide, 1.24 high. Abdomen 5.33 long, 1.79 wide, 1.17 high. Clypeus height equal to one AME diameter. AME diameter 0.12. Sternum 0.93 long, 0.93 wide. Femur I 4.46, 1.6 times the length of the cephalothorax. Vulva as in figures 37D, E, 40B–G.

Variation. Male cephalothorax length varies between 1.96 and 2.30 (n = 20). In females cephalothorax length ranges from 2.20 to 2.84 (n = 10). Total body length in males varies between 5.39 and 6.22 (n=20) and in females between 7.00 and 7.98 (n = 10).

DISTRIBUTION: Panama (Barro Colorado) and Costa Rica (fig. 5).

ADDITIONAL MATERIAL EXAMINED: *Paratypes:* PANAMA: Barro Colorado Island, Canal Zone. viii.1950, A. M. Chickering, 1 female (*allotype*, MCZ 24564); Barro Colorado Island, Canal Zone. 22.vii.1954, A. M. Chickering, 4 males, 5 females (MCZ 24560; 24561, 1 female dissected); Barro Colorado Island, Canal Zone. 15.viii.1954, A.M. Chickering, 1 male, 2 females (MCZ 24562, 24565); Barro Colorado Island, Canal Zone. 16.viii.1954, A. M. Chickering, 1 male (MCZ 24563); Barro Colorado Island, Canal Zone. viii.1939, A. M. Chickering, 1 male (MCZ 24566); Barro Colorado Island, Canal Zone. viii.1936, A. M. Chickering, 2 males (MCZ 24568); Barro Colorado Island, Canal Zone. 8.v.1946, T. C. Schneirla, 1 female (MCZ 24567). *Other material:* PANAMA: Barro Colorado Island, Canal Zone. 8.ii.1958, A. M. Chickering, 1 male (MCZ 66558 used for SEM); Barro Colorado Island, Canal Zone. i.1958, A. M. Chickering, 1 m (MCZ 66559); Barro Colorado Island, Canal Zone. viii.1954, A. M. Chickering, 2 males (MCZ 66560); Barro Colorado Island, Canal Zone. viii.1950, A. M. Chickering, 1 male, 1 female (MCZ 66561); Barro Colorado Island, Canal Zone. v.1964, A. M. Chickering, 3 males (MCZ 66562); Barro Colorado Island, Canal Zone, Zetek trial. 8.ii.1954, A. M. Chickering, 1 male (MCZ 66542). COSTA RICA: San Isidro del General (no date), Dean Reinolds, 1 male (MCZ 66545).

Cyrtognatha rucilla (Bryant, 1945)
Figures 1D, 2A–E, 41–46

Agriognatha rucilla Bryant, 1945: 401, fig. 33.
Agriognatha argyra Bryant, 1945: 397, fig. 35. New synonymy (types examined, see below).
Cyrtognatha rucilla Wunderlich, 1988: 98, fig. 193.
Agriognatha rucilla Dimitrov, Álvarez-Padilla & Hormiga, 2007: 760, figs. 2A–F, 10C–D, 12A.

SYNONYMY JUSTIFICATION: Detailed examination of the type material from *A. argyra* (MCZ 20342) showed that Bryant's drawings accompanying the original description of *A. argyra* are inaccurate. The apical apophysis of the conductor does not have the distinctive semi-spiral curvature depicted in the original illustrations (Bryant, 1945: fig. 35). Furthermore, the rest of the structures of the male palp and the somatic characters are as in *C. rucilla*, and the only difference that can be observed is the size of the specimens. Since body size can vary significantly in *A. rucilla*, such difference in size in the type material of *A. argyra* is deemed insuffcient to consider *A. argyra* as a separate species.

TYPES: *Agriognatha rucilla* male holotype from Dominican Republic, Loma Rucilla Mountains, north of the Cordillera Central, 1500–2400 m. vi.1938, P. J. Darlington (MCZ 22936; examined).

Agriognatha argyra male holotype from Dominican Republic, Valle Nuevo, rain forest, Cordillera Central, 1828 m. vii.1938, P. J. Darlington (MCZ 20342; examined).

DIAGNOSIS: *Cyrtognatha rucilla* is very similar to *C. espanola* and *C. simoni* and this may cause identification problems. The most important male diagnostic character is the shape of the tip of the embolus: in ventral view in *C. rucilla* it is curved retrolaterally (fig. 41A, B), in *C. espanola* it is curved prolaterally, and in *C. simoni* it is almost straight. The shape of the embolus in prolateral view is very characteristic in each of these species and thus it is diagnostic. In *C. rucilla* the embolus is nearly straight prolaterally and its tip is S-shaped (fig. 41C); in *C. espanola* the embolus is arched and the tip of the embolus is additionally curved at almost 90°; *C. simoni* has an embolus that is almost straight, and the tip of the embolus is curved at 90°, as in *C. espanola*.

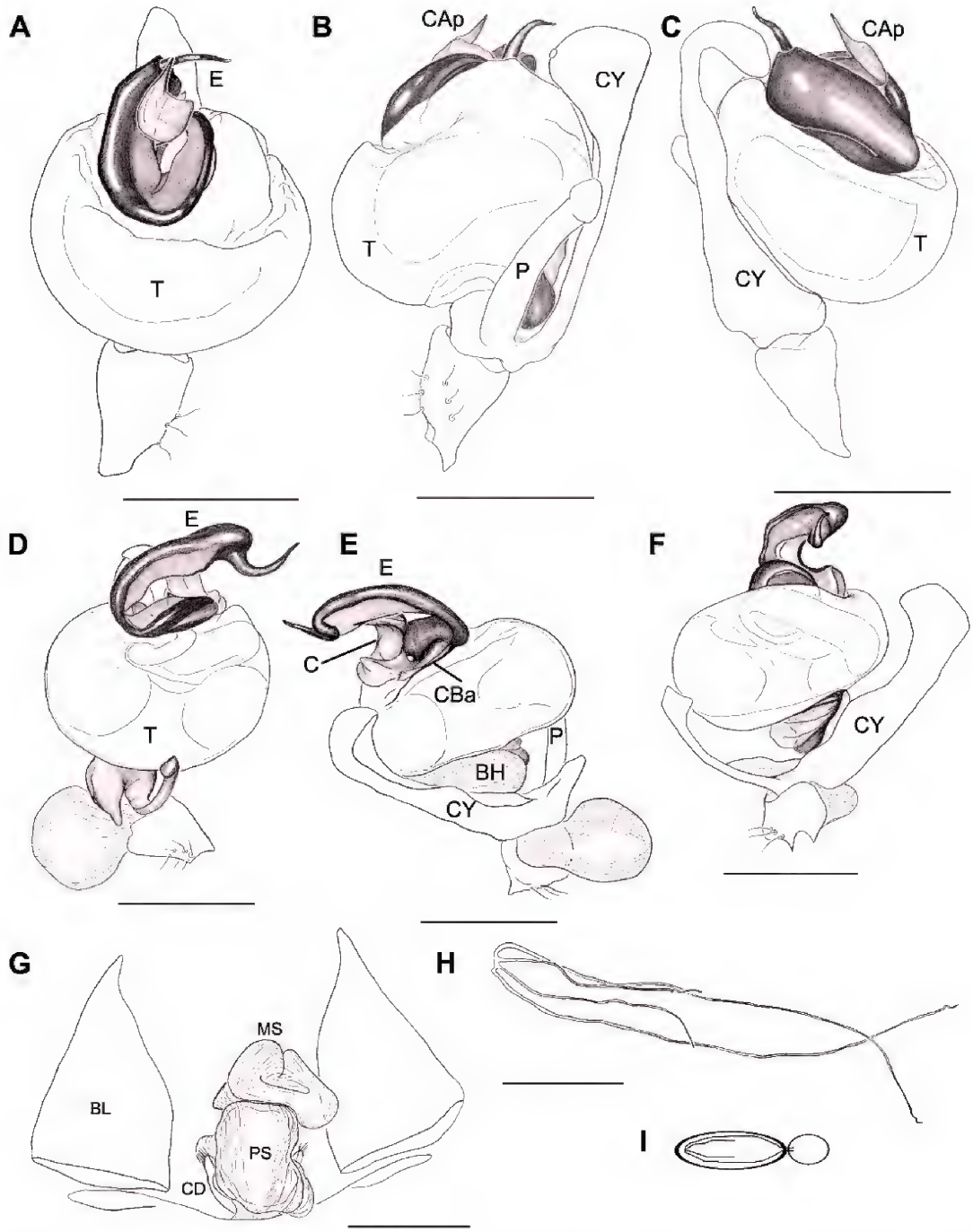

Fig. 41. *Cyrtognatha rucilla*. Male palp: ventral (**A**), retrolateral (**B**), prolateral (**C**). Male palp expanded with KOH (**D–F**) (the tibia-cymbium joint was also affected by the KOH and expanded). Female vulva: dorsal (**G**). Tracheal system (**H** and **I**). Scale bars A–G: 0.5 mm; H: 1 mm.

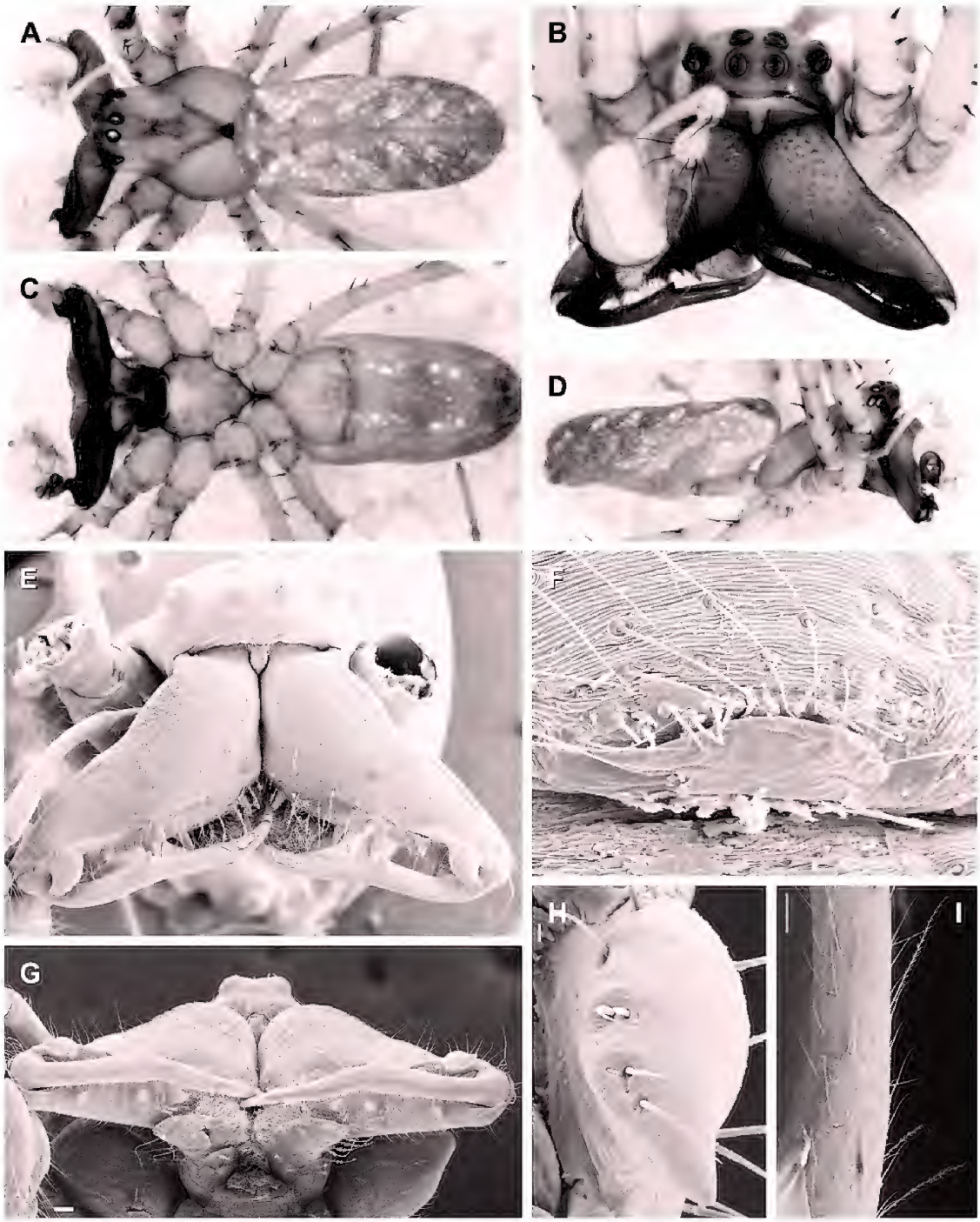

Fig. 42. *Cyrtognatha rucilla*. Male habitus: dorsal (**A**), ventral (**C**), lateral (**D**). Male chelicerae (**B**, **E**, and **G**). Epiandrous fusules (**F**). Cheliceral dorsal tooth (**H**). Female leg IV femur (**I**). Scale bars E, G: 100 μm; F, H, I: 10 μm.

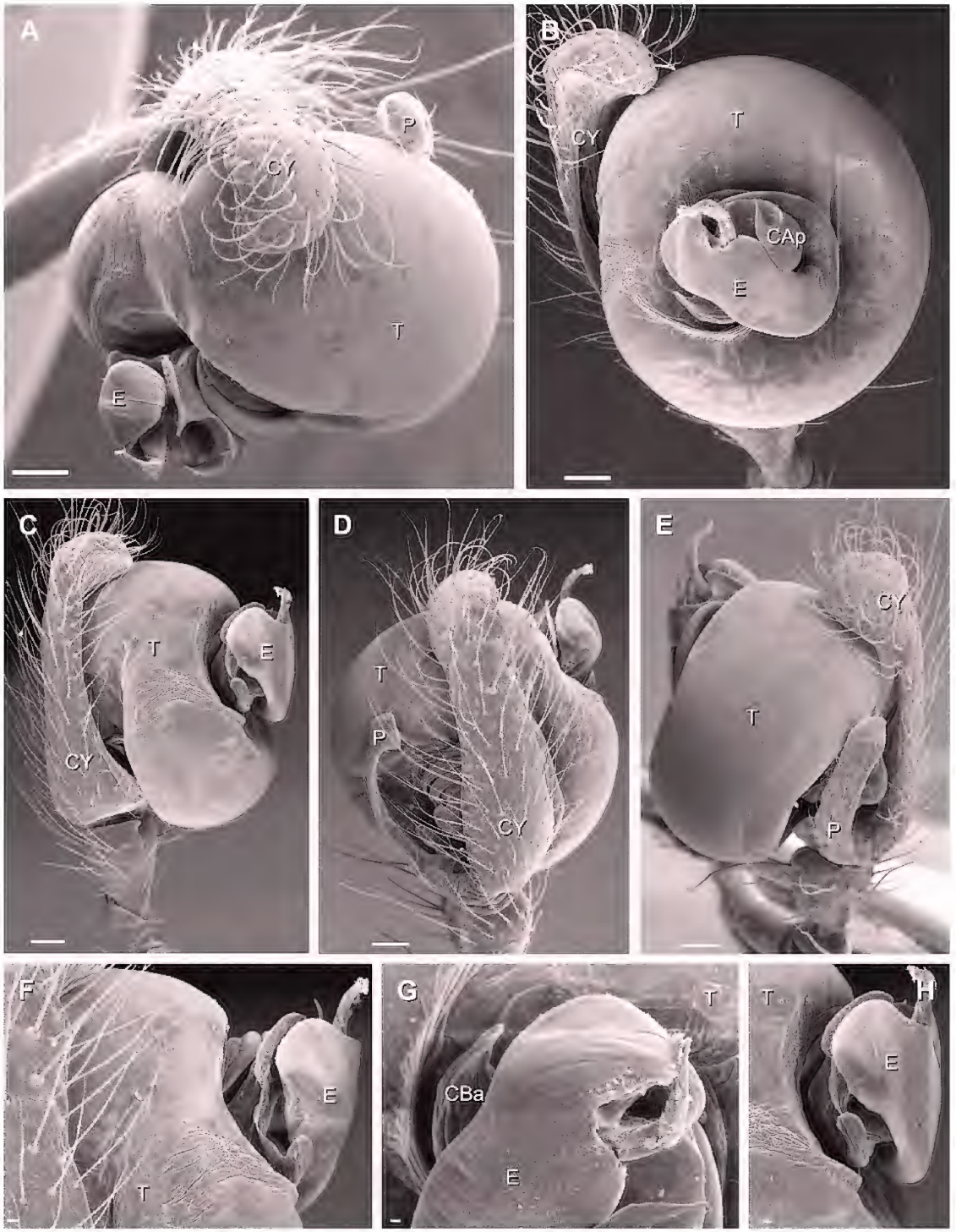

Fig. 43. *Cyrtognatha rucilla*. Male palp: apical (**A**), ventral (**B**), prolateral (**C** and **F**), dorsal (**D**), retrolateral (**E**). Embolus and conductor detail: ventral **G**, prolateral **H** Scale bars A–E 100 μm; F, H 20 μm; G 10 μm.

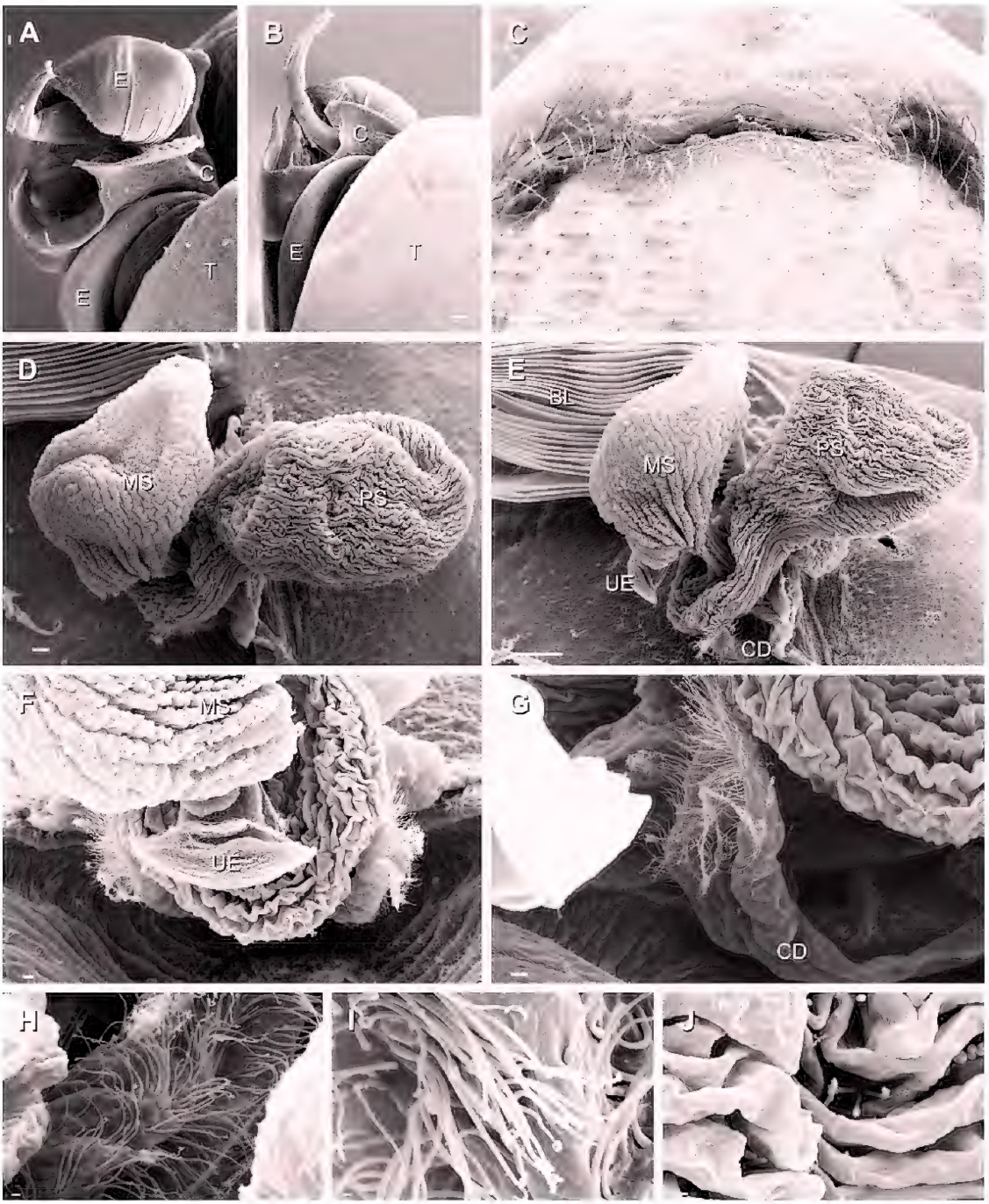

Fig. 44. *Cyrtognatha rucilla*. Male palp: embolus tip apical view (**A**), embolus and conductor in retrolateral view (**B**). Female genital opening: ventral (**C**). Vulva (Dimitrov et al., 2007: fig. 2A): dorsal (**D**), lateral (**E**), frontal (**F**). Copulatory ducts: ultrastructure (**G–I**) (Dimitrov et al., 2007: fig. 2F). Posterior sac cuticle (**J**) (Dimitrov et al., 2007: fig. 2B). Scale bars A, F, G: 10 μm; B: 20 μm; C, E: 100 μm; D: 30 μm; H: 3 μm; I: 1 μm; J: 2 μm.

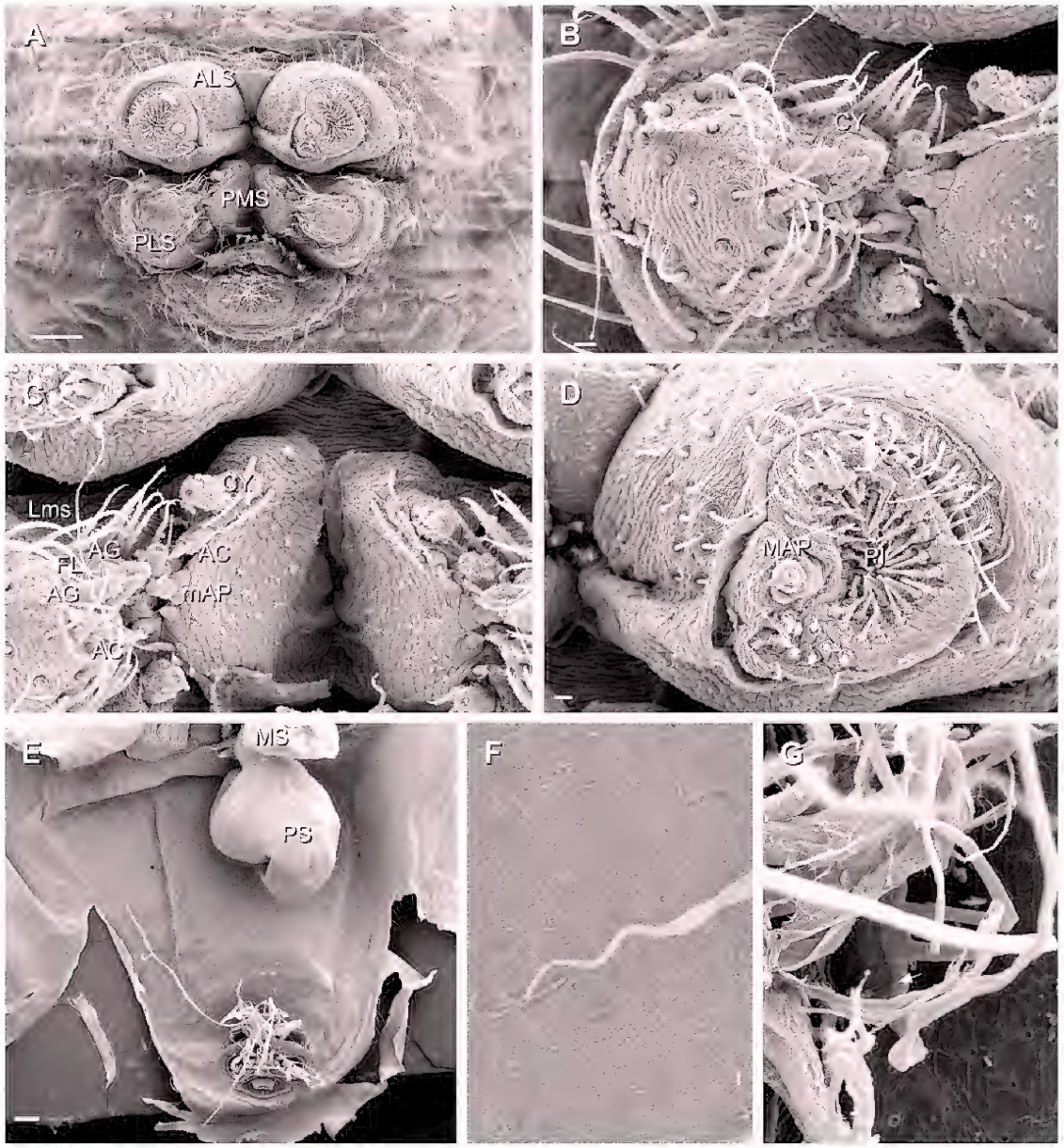

Fig. 45. *Cyrtognatha rucilla*. Female spinnerets: ventral (**A**), PLS (**B**), PLS and PMS (**C**), ALS (**D**). Female tracheal system: vulva and tracheal system: dorsal (**E**), tracheal tip (**F**). Accessory glands around spinnerets: base (**G**). Scale bars A: 100 μm; B–D, F: 10 μm; E: 200 μm; G: 2 μm.

The shape of the male chelicerae provides additional diagnostic characters. In *C. rucilla* the male chelicerae (fig. 42B, E, G) are robust and divergent but the degree of divergence is smaller than in *C. espanola*. *Cyrtognatha simoni* has strongly divergent chelicerae but they are much thinner than in the other two species.

The females of *C. rucilla* can be easily distinguished from closely related species by the size and shape of the sacs in the female vulva (figs. 41G, 44D–G). *Cyrtognatha rucilla* has a median sac, which is almost the same size as the posterior sac, while in *C. espanola* and *C. simoni* the median sac is much smaller than the posterior one.

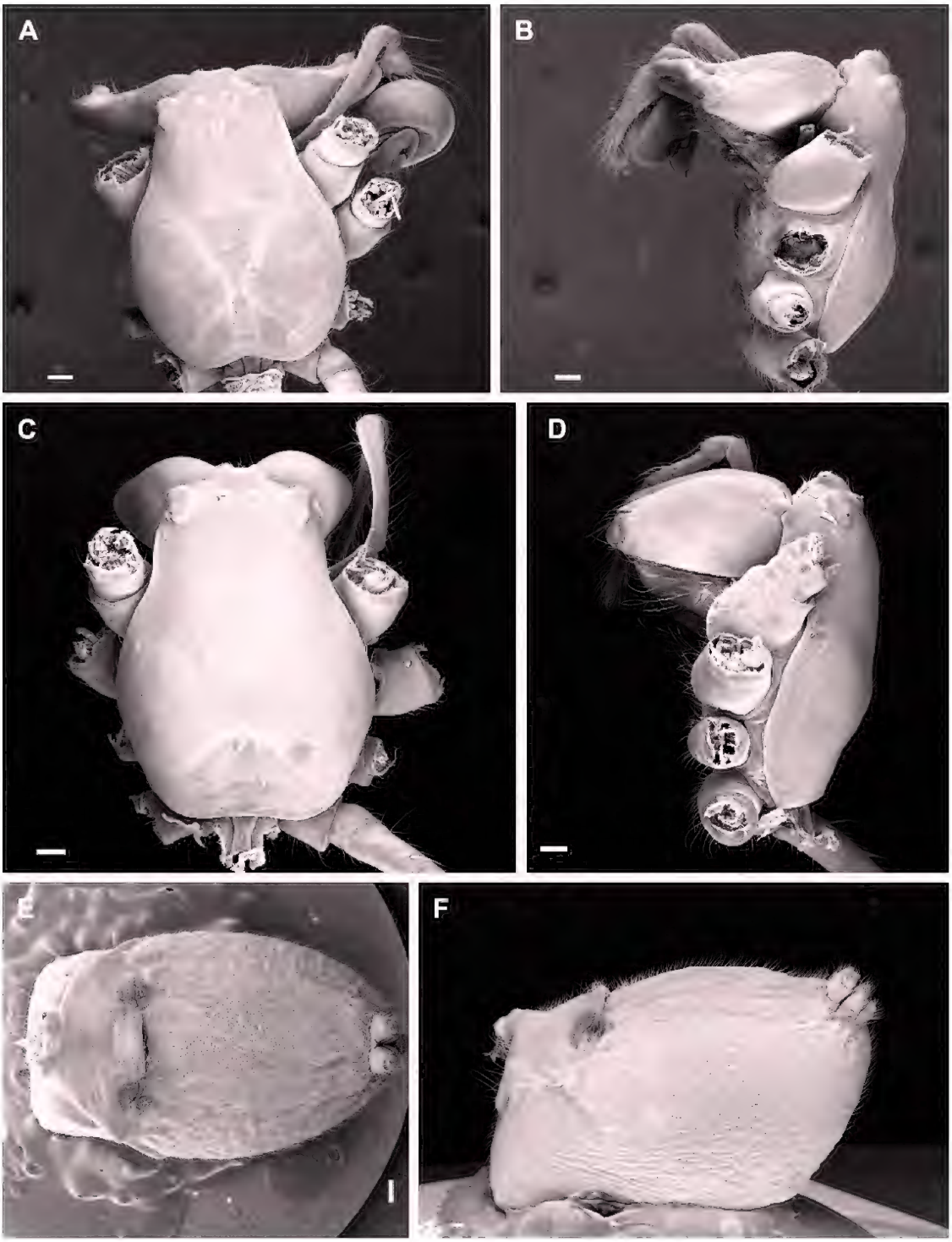

Fig. 46. *Cyrtognatha rucilla*. Male cephalothorax: dorsal (**A**), lateral (**B**). Female cephalothorax: dorsal (**C**), lateral (**D**). Female abdomen: ventral (**E**), lateral (**F**). Scale bars A–E: 200 μm; F: 100 μm.

DESCRIPTION: *Male* (*holotype*). Habitus as in figure 42A–D. Carapace brown-yellowish darker anteriorly and with darker median band and lateral margins. Cephalothorax as in figure 46A, B. Fovea well marked (fig. 46A). Abdomen nearly cylindrical, brown-grayish with numerous guanine spots. The guanine spots are concentrated dorsolaterally and laterally, forming a distinctive pattern. Dorsally with two curvy, darker lines running in parallel. Distal dorsal tubercle reduced; proximal tubercle small. Total length 6.51. Cephalothorax 3.10 long, 1.86 wide, 1.24 high. Abdomen 3.41 long, 1.55 wide, 1.24 high. Sternum yellowish with darker margins with darker bands in front of the coxae; 1.24 long, 1.24 wide. Chelicerae moderately divergent, dark brown. Dorsal tooth large, close to the articulation of the cheliceral fang and with sharp tip curved prolaterally. The tip of the dorsal cheliceral tooth not bifurcated. Cheliceral fang with large outgrowth and distinct curvature before and after it. Chelicerae as in figure 42B, E, G, H. Clypeus height 1.2 times one AME diameter. AME diameter 0.16. AME and AME–PLE one AME diameter. AME–ALE distance more than two AME diameters. Distance between the PLE equal to their diameter. Femur I 5.58, 1.8 times the length of the cephalothorax. Pedipalp as in figures 41A–C, 43A–H, 44A, B. Male palp after expansion with KOH is shown in figure 41D–F. Palpal tibia length 0.25; cymbium length 0.62. Epiandrous fusules as in figure 42F.

Female (*paratype from the type locality*). Habitus and coloration as in male. Chelicerae lighter, yellowish, not divergent, and without dorsal tooth. Abdomen without distal tubercle. Proximal tubercles bigger than in males. Total length 7.44. Cephalothorax (fig. 46C, D) 2.48 long, 1.55 wide, 1.24 high. Abdomen 3.72 long, 1.86 wide, 1.98 high. Sternum darker than in male; 2.91 long, 2.79 wide. Clypeus 0.4 times one AME diameter. AME diameter 0.43. Eyes smaller than in male and PME slightly larger than the rest of the eyes. Vulva as in figures 41G, 44D–G. Copulatory ducts as in figure 44H. Ultrastructure of the copulatory ducts and the cuticle of the posterior sac are shown in figures 44I–J. Leg IV femur as in fig. 42I. Femur I 4.15, 1.67 times the length of the cephalothorax. Tracheal system as in figures 41H, I, 45E, F. Spinnerets as in figure 45A–D. Accessory glands near the spinnerets base (fig. 45G). Abdomen as in figure 46E, F.

Variation. Male cephalothorax length varies from 2.45 to 3.10 (n = 12); in females from 2.20 to 3.40 (n = 32). Total body length in males varies from 5.78 to 6.51 (n = 12); in females between 6.12 and 9.28 (n = 32). Male chelicerae are quite variable in the degree of divergence.

DISTRIBUTION: This species inhabits the Cordillera Central of the Dominican Republic and other high elevation areas of Hispaniola (fig. 5).

ADDITIONAL MATERIAL EXAMINED: *Agriognatha rucilla. Paratypes*: DOMINICAN REPUBLIC: Loma Rucilla Mountains, north of the Cordillera Central, 1500–2400 m, vi.1938, P.J. Darlington, 1 female (*allotype*, MCZ 66564); Loma Vieja, Cordillera Central south of Constanza, viii.1938, P.J. Darlington, 5 females (MCZ 66546); Loma Rucilla Mountains, north of the Cordillera Central, 1500–2400 m, vi.1938, P.J. Darlington, 2 males, 7 females (MCZ 44014).

Agriognatha argyra. Paratypes: DOMINICAN REPUBLIC: Foothills of Cordillera Central south of Sandiago (Santiago?), 600–1500 m. vi.1938, P. J. Darlington, 1 male (MCZ 66547); Loma Rucilla Mountains, north of the Cordillera Central, 1500–2400 m. vi.1938, P. J. Darlington, 1 male (MCZ 66550).

Other material: DOMINICAN REPUBLIC: La Vega Prov., Constanza, Reserva Científica Valle Nuevo, pine forest, 18°46′39.2″N, 70°38′22.4″W, 2277 m, 11.IV.2005, F. Álvarez and S. Benjamin, 6 males, 17 females (MCZ); Barahona Prov., Paraíso, Reserva Natural Cachote, cloud forest and secondary growth, 18°05′54.8″N, 71°11′22.0″W, 1220 m, 6–9.IV.2005, G. Hormiga, F. Álvarez, and S. Benjamin, 1 male, 2 females (MCZ).

Cyrtognatha simoni (Bryant, 1940), new combination
Figures 47–51

Agriognatha simoni Bryant, 1940: 355, figs. 122, 124, 125.

Agriognatha simoni Dimitrov, Álvarez-Padilla & Hormiga, 2007: 762, figs. 4–F, 10C–D.

TYPE: Male holotype from Cuba, Pico Turquino, vi.1936, P. J. Darlington (MCZ 23102; examined).

DIAGNOSIS: *Cyrtognatha simoni* together with *C. espanola* and *C. rucilla* form a group of closely related species that share numerous similarities and are difficult to distinguish. The males can be diagnosed by the shape of the tip of the embolus. In ventral view in *C. simoni* it is almost straight (fig. 47A), in *C. espanola* it is curved prolaterally, and in *C. rucilla* it is curved retrolaterally. The shape of the embolus in prolateral view is also diagnostic. In *C. simoni* the embolus is almost straight and its tip is curved at 90° (fig. 47C); in *C. rucilla* the embolus is nearly straight and its tip is S-shaped; in *C. espanola* the embolus is arched and its tip is additionally curved at almost 90° as in *C. simoni*. The shape of the male chelicerae provides additional diagnostic characters to differentiate these three species. *Cyrtognatha simoni* can be easily distinguished from the other two species by the strongly divergent and much thinner chelicerae (fig. 47H). In *C. rucilla* and *C. espanola* the chelicerae are much more robust. Females of *C. simoni* can be easily distinguished from closely related species by the size and shape of the sacs in the female vulva (figs. 47D, E, 48B, D, F, 49A).

DESCRIPTION: *Male* (*holotype*). Habitus as in figures 47F–H, 48A. Carapace brown-yellowish with darker coloration in the cephalic part. The rest with brown band medially and darker margins. Fovea well marked. Abdomen brown-grayish, cylindrical with few remains of guanine spots. Dorsally with darker line centrally. Laterally with darker markings and ventrally darker with two lighter longitudinal lines. Dorsal tubercles small. Total length 4.65. Cephalothorax 1.86 long, 1.42 wide, 0.99 high. Abdomen 2.79 long, 1.24 wide, 1.24 high. Sternum brownish, lighter adjacent to the labium; 0.87 long, 0.88 wide. Chelicerae dark brown, strongly divergent with well-developed dorsal tooth (figs. 47H, 49B–D). Dorsal tooth close to the fang articulation with sharp tip curved prolaterally. Cheliceral fang with well-developed outgrowth. Clypeus height equal to one AME diameter. AME diameter 0.12. All eyes nearly the same size. Distance between AME equal to their diameter; AME–ALE distance more than twice one AME diameter; AME–PLE distance one AME diameter. Distance between PLE less than their diameter. Femur I 4.96, 2.7 times the length of the cephalothorax. Pedipalp as in figures 47A–C, 50C–G, 51A–J. Palpal tibia length 0.25; cymbium length 0.81. Epiandrous fusules as in figure 49E. Spinnerets as in figures 49F–H, 50A, B.

Female (*paratype from the type locality*). Habitus and color pattern as in male but cephalothorax yellowish and lighter in color, with darker band medially. Chelicerae not divergent and without dorsal tooth. Total length 6.69. Cephalothorax 2.35 long, 1.73 wide, 1.24 high. Abdomen 4.32 long, 2.10 wide, 2.48 high. Sternum 1.05 long, 0.92 wide. Clypeus height 0.6 times one AME diameter. AME diameter 0.12. Femur I 3.72, 1.5 times the length of the cephalothorax. Vulva as in figures 47D, E, 48B–F, 49A.

Variation. Cephalothorax length varies from 1.86 to 1.98 in males (n = 6) and from 2.29 to 2.48 in females (n = 3). Total body length in males varies from 4.09 to 4.58 (n = 6) and in females from 5.20 to 6.94 (n = 3).

DISTRIBUTION: Eastern Cuba, Santiago de Cuba and Guantanamo provinces (fig. 5).

ADDITIONAL MATERIAL EXAMINED: *Paratypes:* CUBA: Pico Turquino. vi.1936, P. J. Darlington, 1 female (*allotype*, MCZ 26241); Pico Turquino, vi 1936, P. J. Darlington, 4 males, 4 females (MCZ 26242 1 female dissected); mountains north of Imias, 914–1219 m. vi.1936, P. J. Darlington, 1 male, 2 females (MCZ 26243 male used for SEM).

Cyrtognatha bryantae (Chickering, 1956), new combination
Figures 52–57

Agriognatha bryantae Chickering, 1956a: 2, figs. 1–5.

TYPE: Male holotype from Jamaica, Hardwar Gap, 27.vi.1954, A. M. Chickering (MCZ 20613; examined).

DIAGNOSIS: *Cyrtognatha bryantae* can be easily distinguished from similar congeners (*C. espanola* and *C. simoni*) by the arched embolus, which has a semitransparent membrane in prolateral view (fig. 52C). The latter two species lack such membrane. Further-

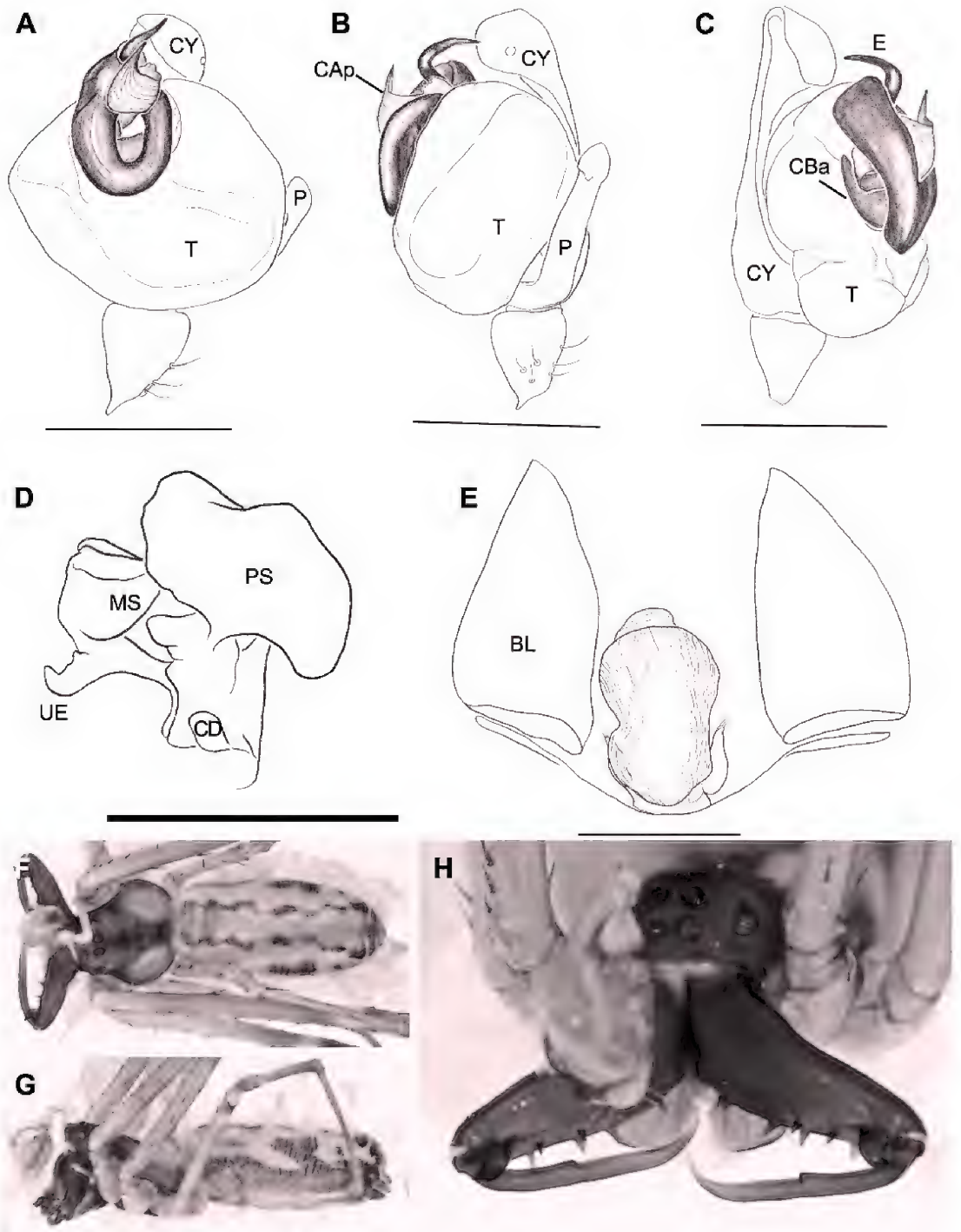

Fig. 47. *Cyrtognatha simoni.* Male palp: ventral (**A**), retrolateral (**B**), prolateral (**C**). Vulva: lateral (**D**), dorsal (**E**). Male habitus: dorsal (**F**), lateral (**G**). Male chelicerae (**H**). Scale bars 0.5 mm.

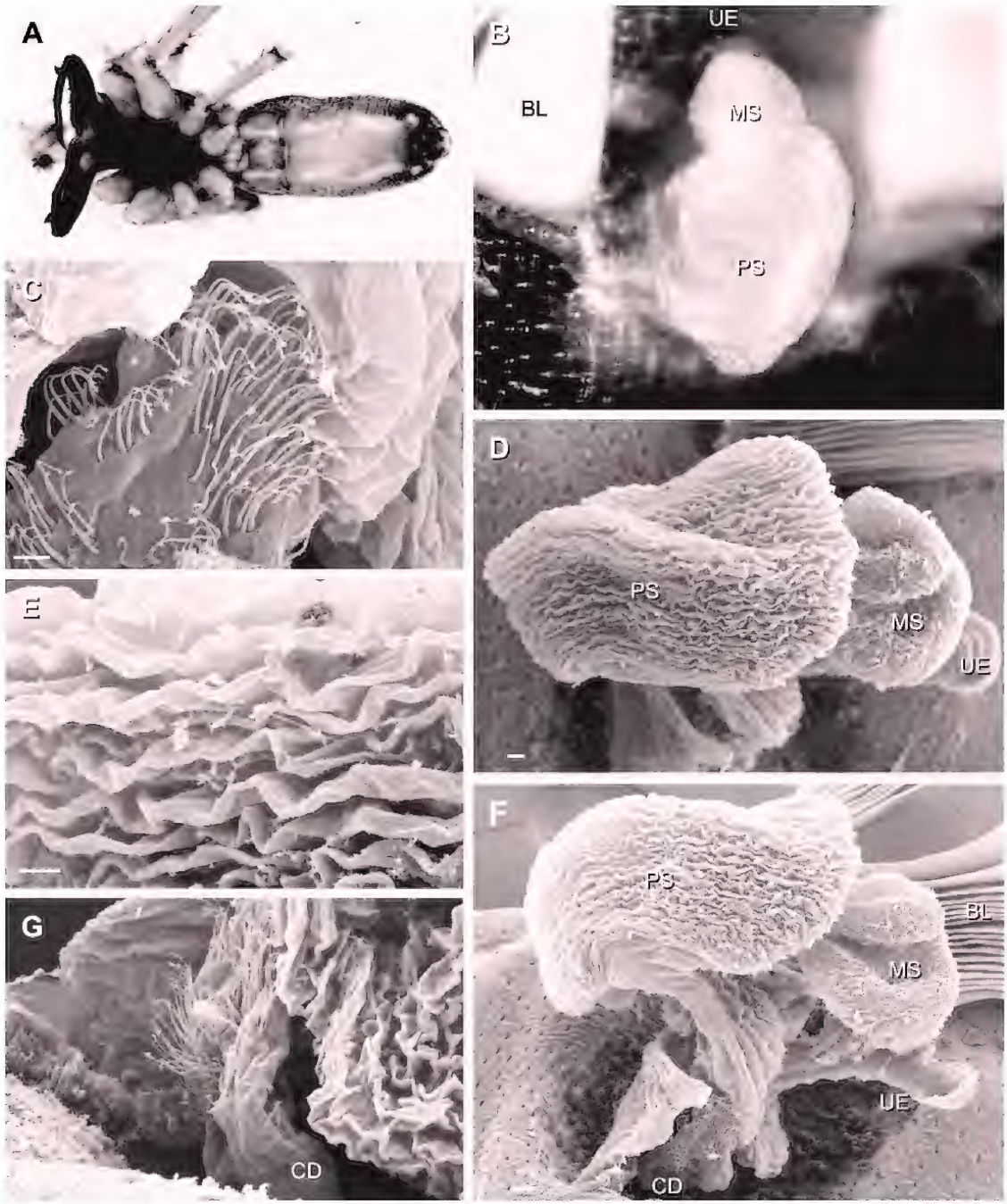

Fig. 48. *Cyrtognatha simoni*. Male: dorsal (**A**). Vulva: lateral (**B**). Vulva: copulatory ducts close look (**C**), vulva dorsal (**D**), posterior sac cuticle (**E**), vulva lateral (**F**) (fig. 4F, A, and B, respectively, of Dimitrov et al., 2007). Copulatory ducts frontal (**G**). Scale bars: C, E, G: 10 μm; D: 20 μm; F: 30 μm.

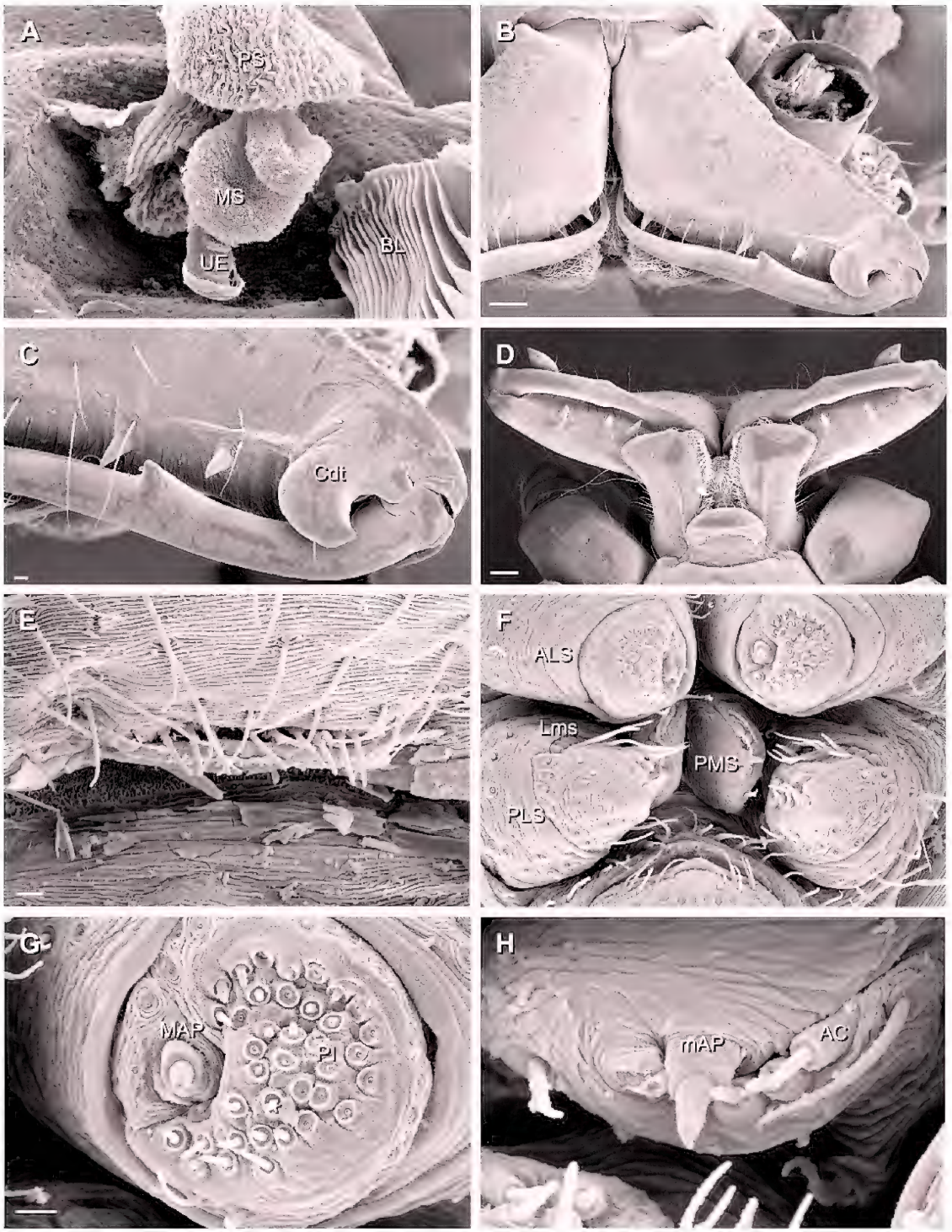

Fig. 49. *Cyrtognatha simoni*. Female vulva: frontal (**A**). Male chelicerae (**B–D**). Epiandrous fusules (**E**). Male spinnerets (**F**). Male ALS (**G**). Male PMS (**H**). Scale bars A: 30 μm; B, D: 100 μm; C, E–G: 10 μm; H: 2 μm.

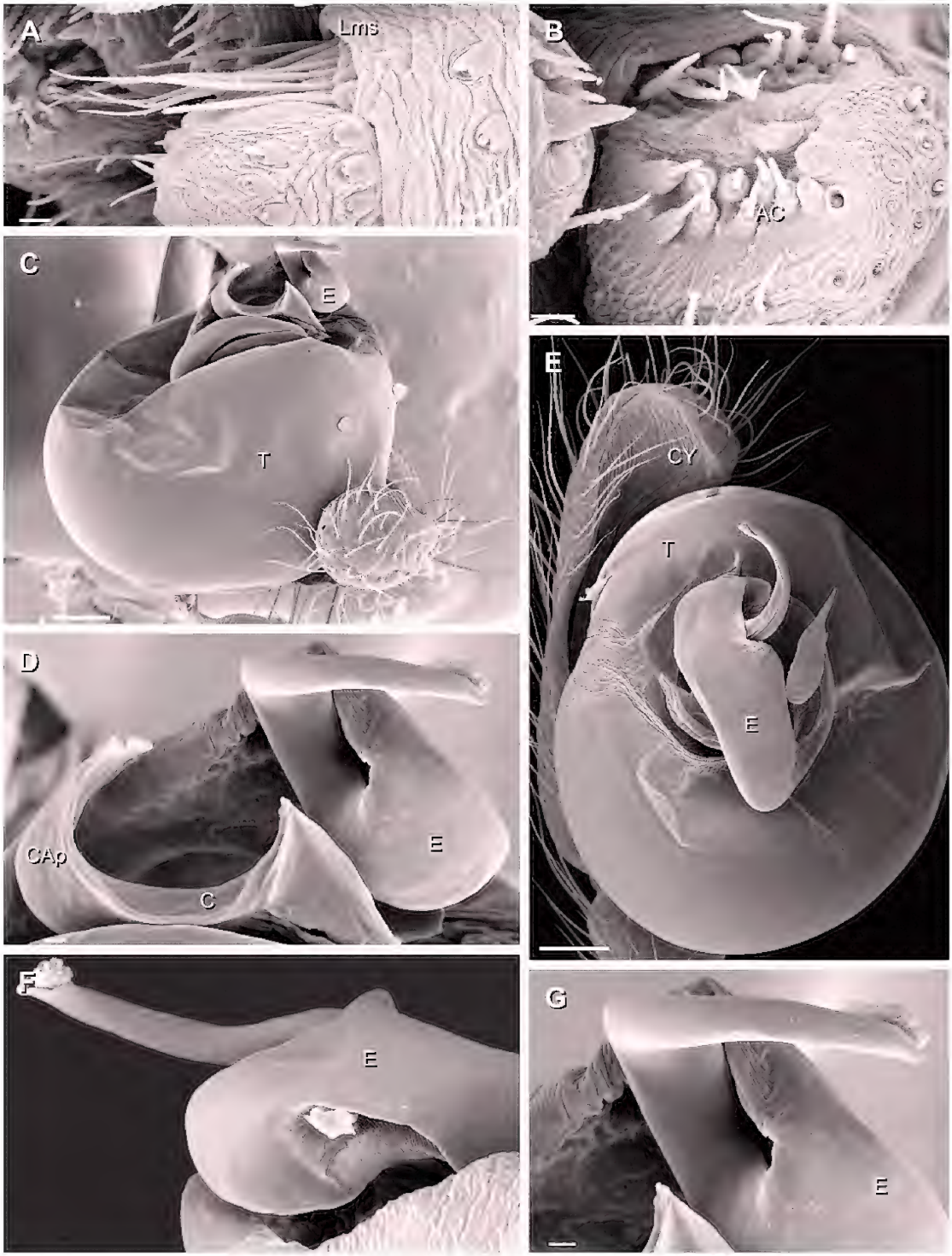

Fig. 50. *Cyrtognatha simoni*. Male PLS: lateral (**A**), ventral (**B**). Male palp: apical (**C**), ventral (**E**). Conductor and embolus apically (**D**). Tip of the embolus prolateral (**F**). Tip of the embolus: apical (**G**). Scale bars A, B, D, F, G: 10 μm; C, E: 100 μm.

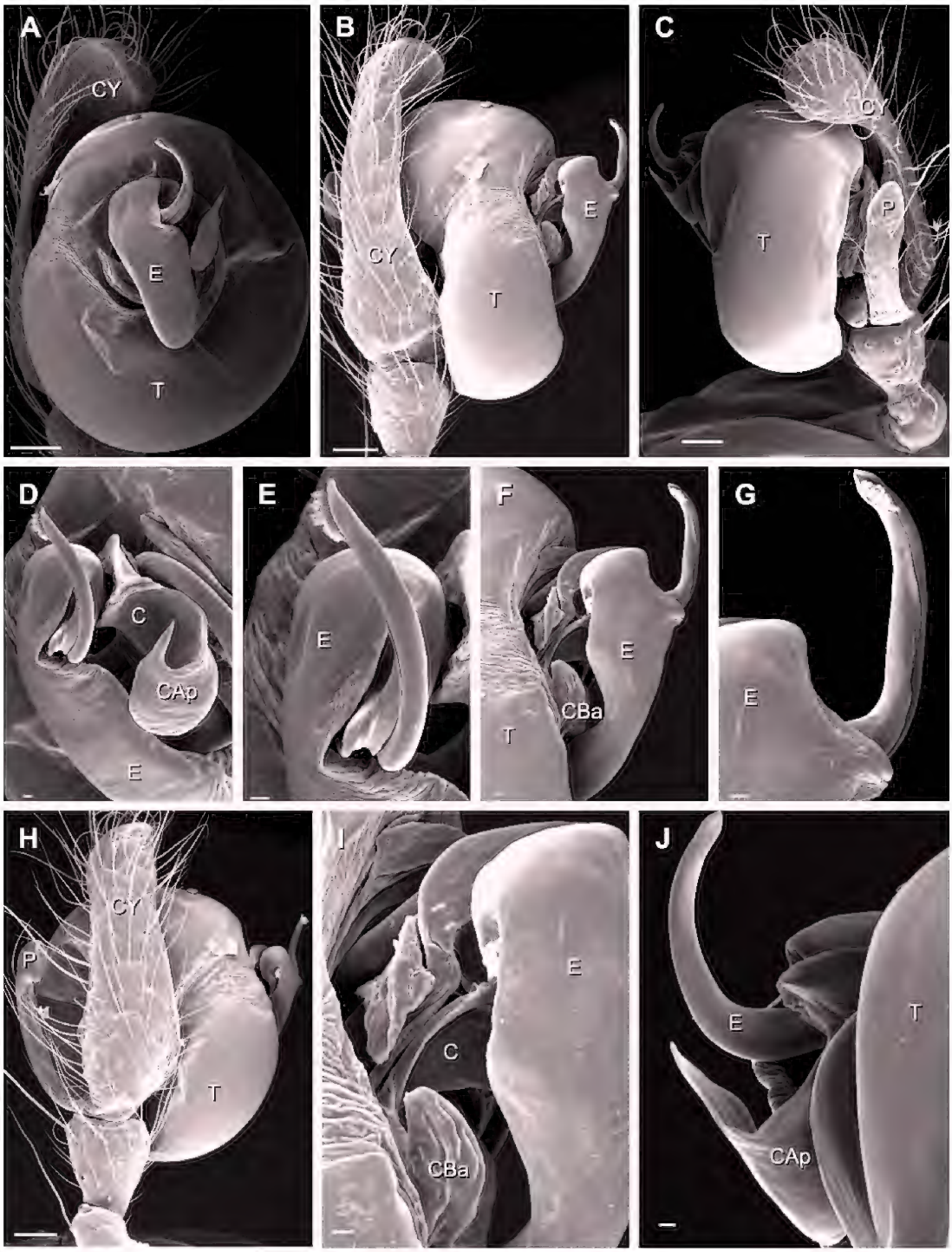

Fig. 51. *Cyrtognatha simoni*. Male palp: ventral (**A**), prolateral (**B**), retrolateral (**C**), dorsal (**H**). Embolus and conductor: ventral (**D**). Tip of the embolus: ventral (**E**). Embolus and conductor: prolateral (**F**). Tip of the embolus: prolateral (**G**). Embolus and conductor base in prolateral view (**I**). Embolus and conductor: retrolateral (**J**). Scale bars A, B, C, H: 100 μm; D: 20 μm; E, F, G, I, J: 10 μm.

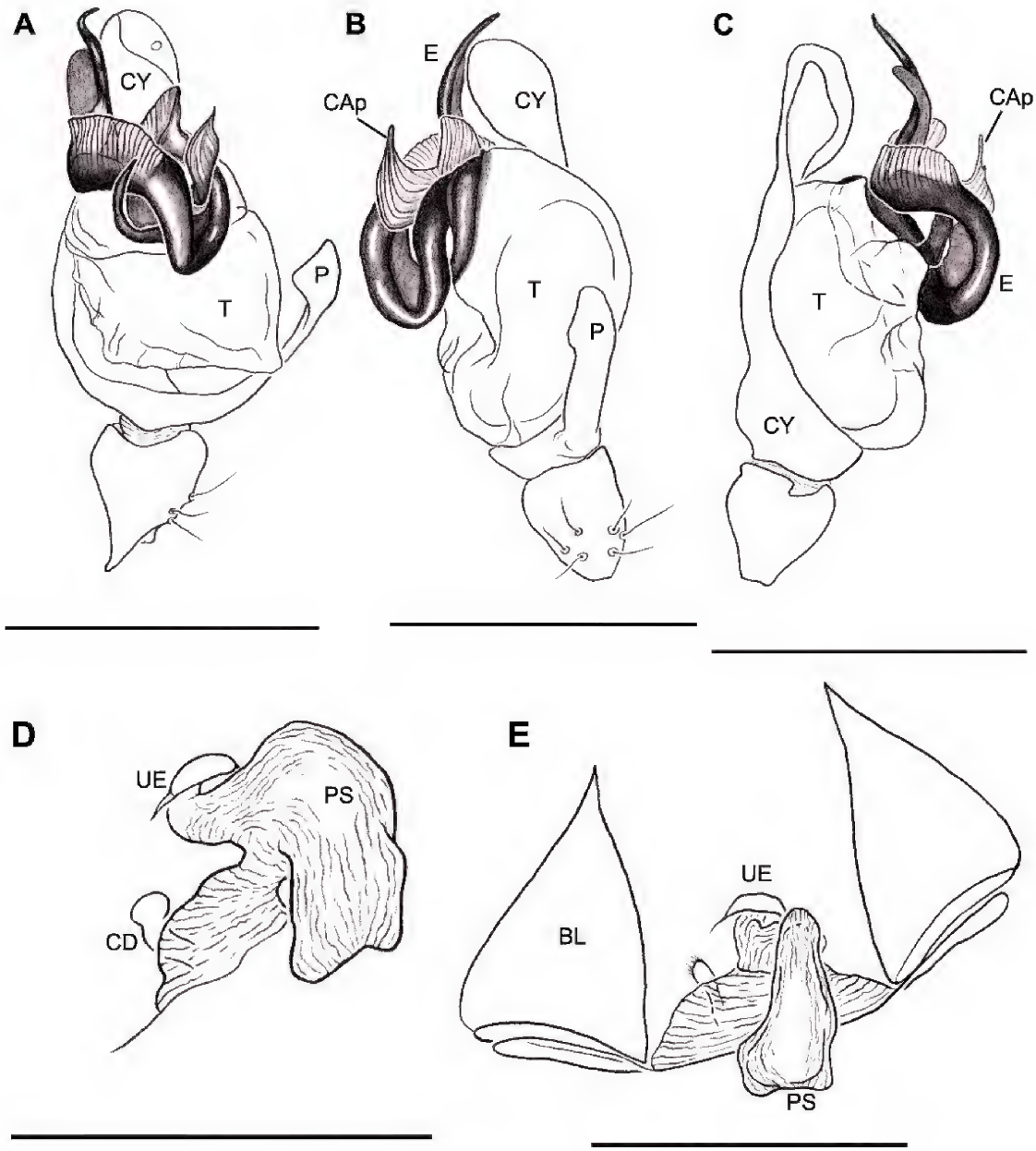

Fig. 52. *Cyrtognatha bryantae*. Male palp: ventral (**A**), retroalteral (**B**), prolateral (**C**). Female vulva: lateral (**D**), dorsal (**E**). Scale bars 0.5 mm.

more, *C. bryantae* differs from *C. espanola* and *C. simoni* in the shape of the paracymbium and in having the larger part of the embolus thinner distally (fig. 52A, C). Males can be also easily distinguished by the cylindrically shaped abdomen and the smaller distal tubercle of the abdomen. The females of these three species show significant differences in the morphology of the internal female genitalia. In *C. bryantae* (figs. 52D, E, 54A–D, G) the posterior sac is longer and widened distally and the median sac is absent. Both *C. espanola* (fig. 31D, E) and *C. simoni* (fig. 47D, E) have median sac.

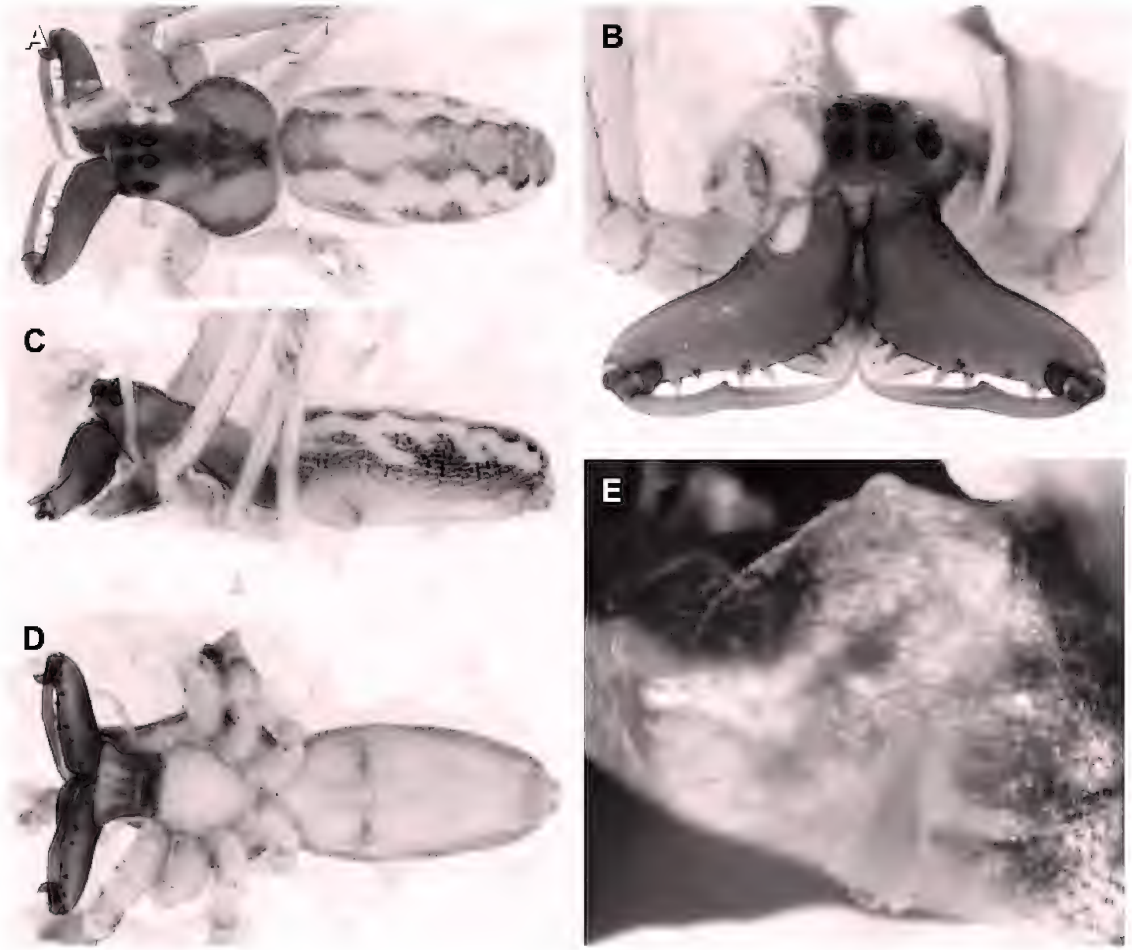

Fig. 53. *Cyrtognatha bryantae*. Male habitus: dorsal (**A**), lateral (**C**), ventral (**D**). Male chelicerae (**D**). Vuvla dorsal (**E**).

DESCRIPTION: *Male* (*holotype*). Habitus as in figure 53A–D. Carapace brown, darker frontally with dark brown edges and with darker pigmentation starting at the PLE, which extends centrally, reaching the fovea. Fovea well marked. Abdomen elongated, gray-brownish and with greenish tones. Reflecting guanine spots almost completely lost in this specimen (but present in paratypes). Dorsally with distinctive pattern centrally (fig. 53A), delimited by lighter grayish longitudinal lines. Total length 4.00. Cephalothorax 1.75 long, 1.32 wide, 0.87 high. Abdomen 2.25 long, 1.17 wide, 1.00 high. Sternum yellowish with darker margins; 0.87 long, 0.80 wide. Clypeus height one AME diameter. AME diameter 0.12. Distance between AME slightly larger than their diameter; AME–ALE distance 2.5 times one AME diameter; AME–PME distance 1.5 times one AME diameter. Distance between PME equal to their diameter. All eyes surrounded by darker pigmentation. Chelicerae (figs. 53B, 55A–C) dark brownish, divergent with a well-developed dorsal tooth. Dorsal tooth close to the fang articulation, with sharp tip and with a very well-pronounced prolateral curvature. Chelicerae fang with well-developed outgrowth. Femur I 3.72, 2.1 times the length of the cephalothorax. Pedipalp as in figures 52A–C, 55E–G, 56A–F. Palpal tibia length 0.17; cymbium length 0.75. Epiandrous fusules as in figure 55D. Leg IV femur as in figure 54I. Spinnerets as in figures 56G, 57A–C.

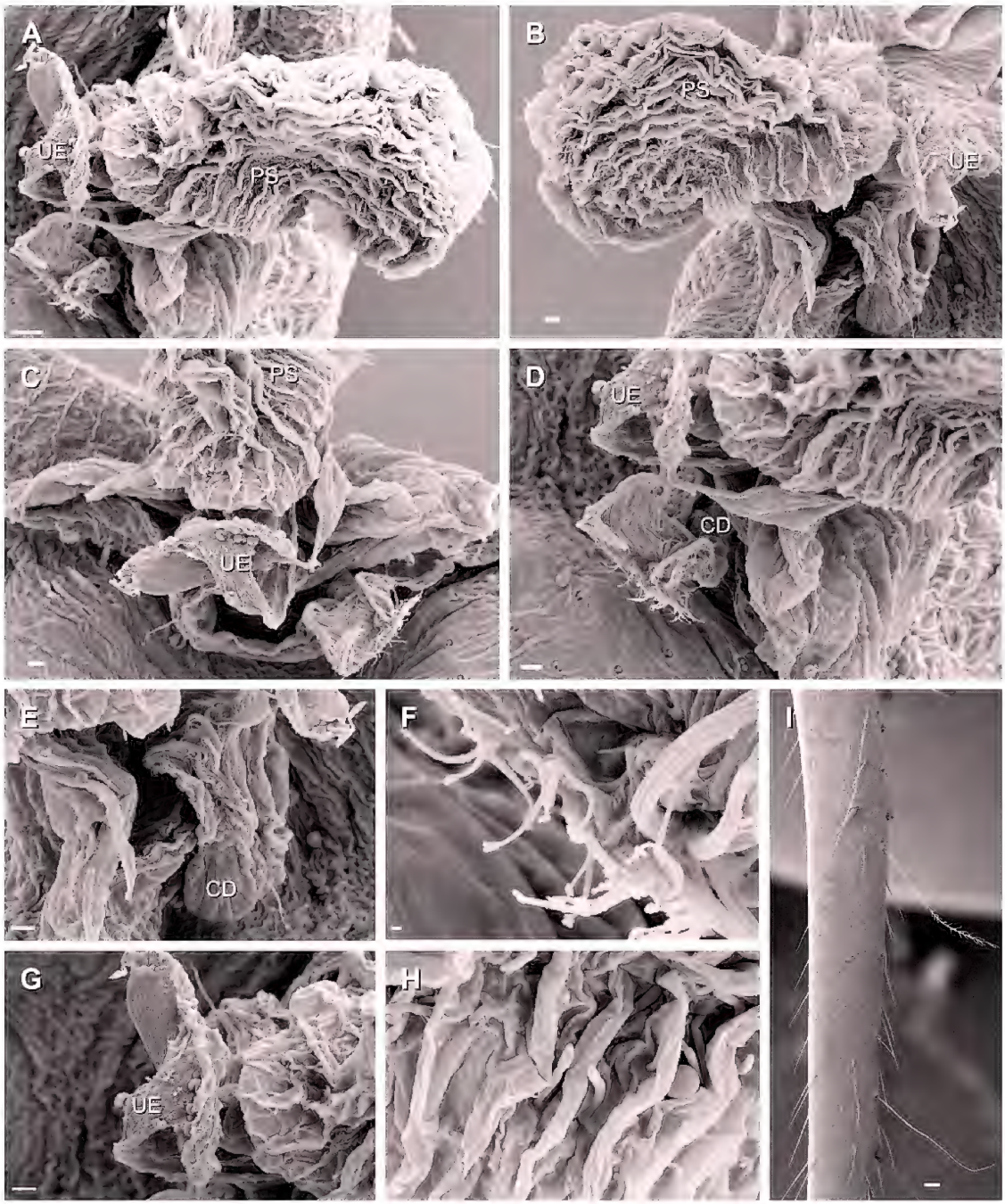

Fig. 54. *Cyrtognatha bryantae*. Female vulva: dorsal (**A**), dorsolateral (**B**), frontal (**C**). Copulatory ducts: dorsolateral (**D**), lateral (**E**). Long ductule glands (**F**). Uterus: externus (**G**). Posterior sac cuticle (**H**). Male leg IV femur (**I**). Scale bars A: 20 μm; B–E, G: 10 μm; F, H: 1 μm; I: 30 μm.

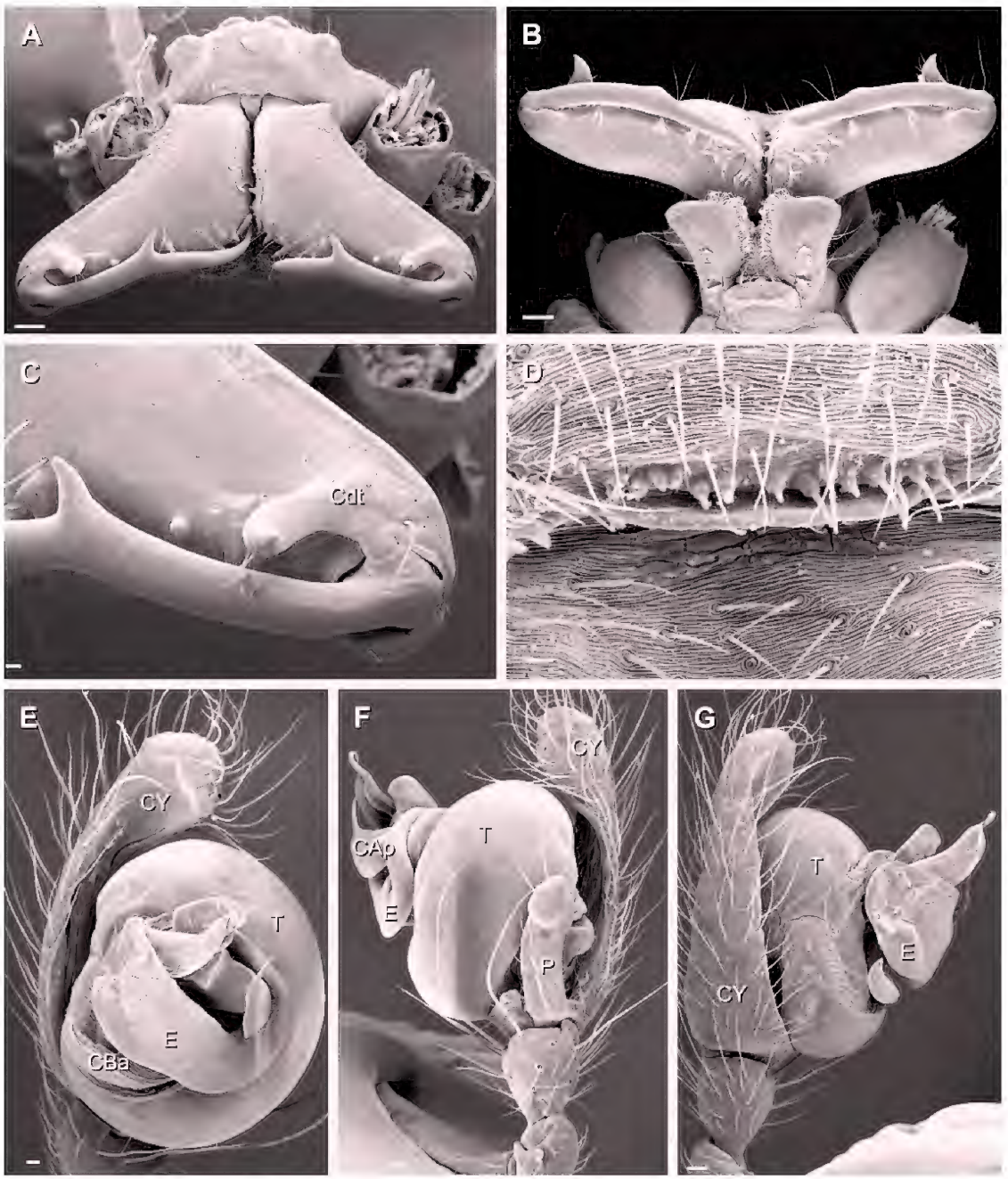

Fig. 55. *Cyrtognatha bryantae*. Male chelicerae: frontal (**A**), ventral (**B**). Male cheliceral dorsal tooth (**C**). Epiandrous fusules (**D**). Male palp: ventral (**E**), retrolateral (**F**), prolateral (**G**). Scale bars A, B: 100 μm; C, E: 20 μm; D: 10 μm; F, G: 30 μm.

Female (*paratype from the type locality*). Habitus and coloration as in male. Abdomen with a well-developed conical distal tubercle, which is situated in its distal third. Chelicerae not divergent, lighter colored, and without dorsal tooth. Total length 5.14. Cephalothorax 1.86 long, 1.55 wide, 0.93 high. Abdomen 3.28 long, 1.65 wide, 2.17

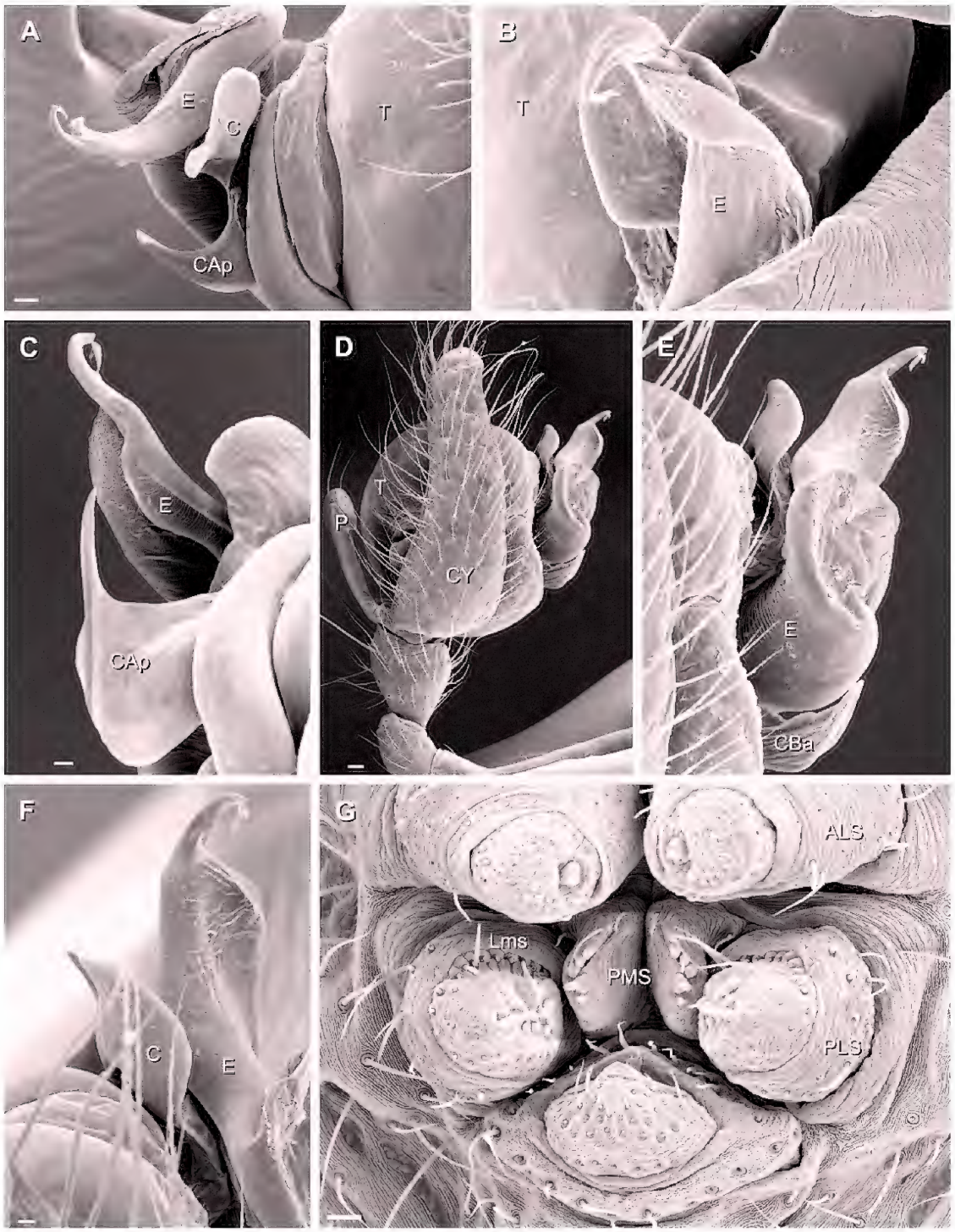

Fig. 56. *Cyrtognatha bryantae*. Conductor and embolus apically (**A**). Tip of the embolus apically (**B**). Conductor and embolus: retrolateral (**C**). Male palp: dorsal (**D**). Conductor and embolus: prolateral (**E**). Embolus tip: prolateral (**F**). Male spinnerets: ventral (**G**). Scale bars A–C, E–G: 20 μm; D: 30 μm.

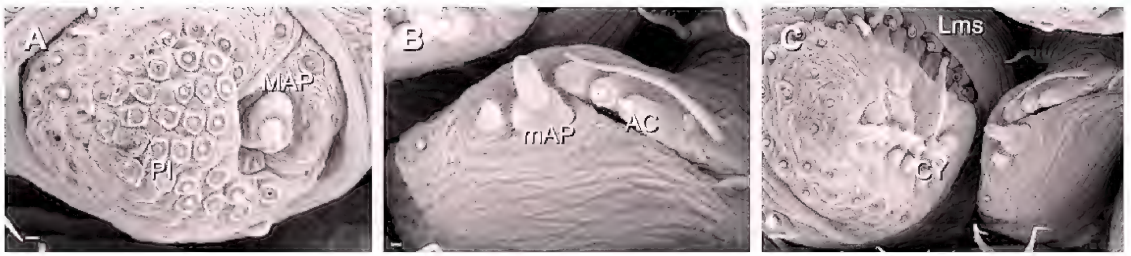

Fig. 57. *Cyrtognatha bryantae*. Male spinnerets: ALS (**A**), PMS (**B**), PLS and PMS (**C**). Scale bars A: 3 μm; B: 2 μm; C: 10 μm.

high. Sternum darker colored than in male; 0.93 long, 0.93 wide. Clypeus height 0.3 times one AME diameter. AME diameter 0.11. Femur I 1.86, equal to the length of the cephalothorax. Vulva as in figures 52D, E, 53E, 54A–H.

Variation. Cephalothorax length varies from 1.22 to 1.75 in males (n = 32) and from 1.81 to 1.96 in females (n = 27). Total body length varies from 3.18 to 4.00 in males (n = 32) and from 4.60 and 5.39 in females (n = 27).

DISTRIBUTION: This species in known only form the island of Jamaica (fig. 5).

ADDITIONAL MATERIAL EXAMINED: *Paratypes:* JAMAICA: Hardwar Gap, 27.vi.1954, A. M. Chickering, 1 female (*allotype*, MCZ 20613); Hardwar Gap, 24.vi.1954, A. M. Chickering, 4 males, 3 females (MCZ 24555); Hanover Parish, Askenish, trail to Dolphins Head, 24.vi.1954, A. M. Chickering, 1 male, 1 female (MCZ 24556); Hardwar Gap, 27.vi.1954, A. M. Chickering, 1 male, 2 females (MCZ 24559); Blue Mts., Main Range, 1524–2133 m, vii.1934, P. J. Darlington, 6 males, 2 females (MCZ 24554, 24558); Blue Mts., SW side of the Main Range, 914–1219 m, 13.vii.1934, P. J. Darlington, 3 males, 6 females (MCZ 24557, one of the females dissected); Hardwar Gap, Portland Parish, 1402 m. 28.iv.1955, A. F. Archer, 2 females (AMNH). *Other material:* JAMAICA: Hardwar Gap, St. Andrew Parish, 2.x.1957, A. M. Chickering, 4 males (MCZ 66553, one male used for SEM); Hanover Parish, Askenish, trail to Dolphins Head, 24.vi.1956, A. M. Chickering, 1 male subadult (MCZ 66554); St. Andrew Parish, Hermitage reservoir, 5.xi.1957, A. M. Chickering, 5 males, 1 female (MCZ 66555); St. Andrew Parish, Hermitage reservoir. 30.x.1957, A. M. Chickering, 2 males (MCZ 66556); St. Ann Parish, 3 miles S. Moneague, St. Ann's Bay Rd, 7.xi.1957, A. M. Chickering, 1 male (MCZ 66557); Portland Parish, Yseen Hills (Yaseen?), 12.xi. 1963, A. M. Chickering 1 male, 1 female (MCZ 66539); Hardwar Gap. 22.ii.1955, A. M. Nadler, 1 male (AMNH); Hardwar Gap, Portland Parish, 1402 m. 28.iv.1955, A.F. Archer, 1 male (AMNH); Hardwar Gap, 17.iii.1955, A. M. Nadler, 1 male, 2 females (AMNH); Hardwar Gap. 6.xii.1954, A.M. Nadler, 1 female (AMNH); Portland, John Crown Mts., 7 mi. WSW of Ecclesdown, 17.viii.1958, Archer, Carr, and Bergey 2 females, 1 male subadult (AMNH); Hardwar Gap, Portland Parish, 1402 m. 28.vii.1953, A. F. Archer, 2 male palps in the vial, 3 females (AMNH)

Cyrtognatha bella (O. P.-Cambridge, 1896)
Figure 58

Agriognatha bella O. P.-Cambridge, 1896: 213, pl. 28, fig. 7.
Cyrtognatha bella Petrunkevitch, 1911: 335.

TYPE: Male holotype from Costa Rica, no collector or date on the label (BMNH 1905.4. 28.2229; examined).

DIAGNOSIS: *Cyrtognatha bella* shares numerous similarities with the closely related *C. leviorum*, but it can be easily distinguished from the latter by the membranous basal apophysis of the conductor and the absence of metine embolic apophysis (fig. 58A, B). Additionally, the male chelicerae of *C. bella* (fig. 58E) are much more divergent than those of *C. leviorum*.

DESCRIPTION: *Male* (*holotype*). Habitus as in figure 58D–G. Carapace yellow-brownish

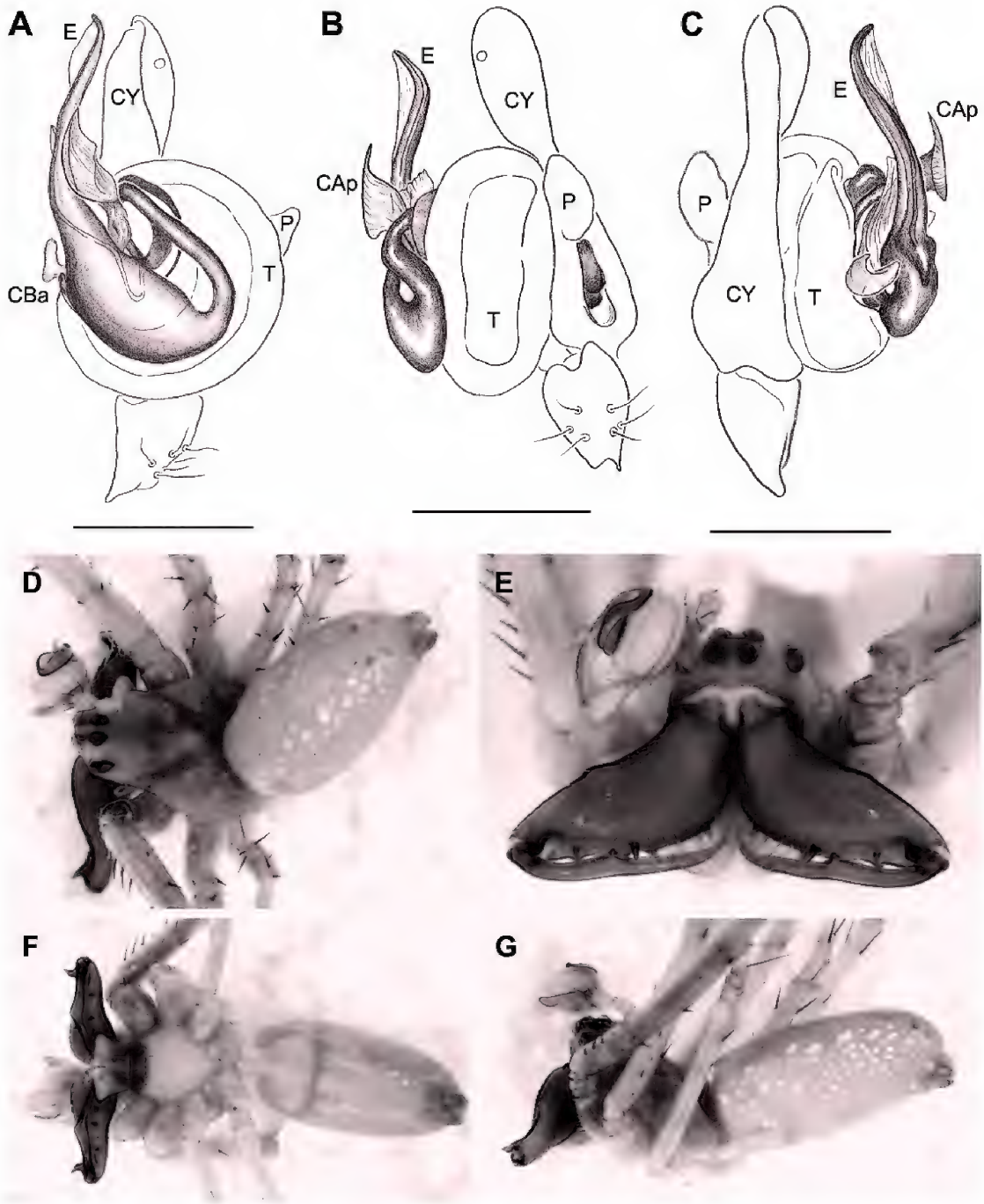

Fig. 58. *Cyrtognatha bella*. Male palp: ventral (**A**), retrolateral (**B**), prolateral (**C**). Male habitus: dorsal (**D**), ventral (**F**), lateral (**G**). Male chelicerae (**E**). Scale bars 0.5 mm.

with a well-marked fovea. Abdomen elongated, yellowish, and with guanine spots concentrated dorsolaterally. Proximal and dorsal tubercle very small. Sternum yellowish. Labium and basal part of the endites darker with brownish tones. Sternum 0.92 long, 0.88 wide. Total length 4.57. Cephalothorax 2.00 long, 1.37 wide, 1.12 high. Abdomen 2.57 long, 1.25 wide, 1.25 high. Chelicerae (fig. 58E) dark brown, strong, and widely divergent. Cheliceral teeth very robust; dorsal tooth well developed and curved prolaterally. Cheliceral fang with large outgrowth. Clypeus 1.5 times one AME diameter. AME diameter 0.10. Eyes nearly the same size. Lateral eyes on a well-developed elevations. Distance between AME equal to their diameter; AME–ALE distance more than twice the AME diameter. Distance between PME equal to their diameter. Femur I 3.67, 1.83 times the length of the cephalothorax. Pedipalp as in figure 58A–C. Palpal tibia length 0.30; cymbium length 0.88.

Female. Unknown.

DISTRIBUTION: Costa Rica (fig. 5).

ADDITIONAL MATERIAL EXAMINED: *Other material*: Costa Rica, 1920, P. Serra, 1 male (MNHN 24871).

Cyrtognatha lepida (O. P.-Cambridge, 1889) Figure 59

Argyroepeira lepida O. P.-Cambridge, 1889: 7, pl. 1, fig. 8.
Agriognatha lepida F. O. P.-Cambridge, 1903: 437.
Cyrtognatha lepida Petrunkevitch, 1911: 335.

TYPE: Female holotype; no collector and date (BMNH 1905.4.28.2230–2232; examined). In the original description (O. P. -Cambridge, 1889) the locality cited for this species is Bugaba, Panama. Holotype disarticulated and in poor condition.

DIAGNOSIS: The morphology of the internal genitalia of *C. lepida* is very similar to that of *C. paradoxa* and *C. pathetica*. *Cyrtognatha lepida* can be distinguished from *C. pathetica* by the presence in the former of a characteristic longitudinal marking on the abdomen and the widened tips of the copulatory ducts (fig. 59B). The basal chamber connecting the genital opening with the membranous sacs in *C. lepida* (fig. 59A, B) is flattened and much longer than that in *C. pathetica* and *C paradoxa*.

DESCRIPTION: *Male*. Unknown.

Female (*holotype*). Carapace brown-yellowish with a well-marked fovea. Dorsally with dark brown band medially and with darker coloration at the margins. Abdomen elongated with brown-grayish coloration and with numerous guanine spots (fig. 59C). Dorsally with two brown colored, irregular longitudinal lines. The lateral sides with brownish markings. Proximal tubercles moderately pronounced; distal tubercle small, darker over the spinnerets. Spinnerets surrounded by dark brown pigmentation. Relatively large spiders; total length 10.73. Cephalothorax 3.43 long, 1.96 wide, 1.47 high. Abdomen 7.30 long, 2.94 wide, 2.84 high. Sternum yellowish; 1.42 long, 1.37 wide. Labium and lateral sides of the endites darker with brownish coloration. Clypeus height 1.13 times one AME diameter. AME diameter 1.50. Eyes nearly the same size. Lateral eyes placed very close together (practically touching each other) on small elevations. Distance between AME almost equal to their diameter; distance between AME and ALE nearly three times the AME diameter. Distance between PLE equal to their diameter. Legs relatively long, with darker bands near the articulations. Femur I 5.88, 1.7 times the length of the cephalothorax. Vulva as in fig. 59A, B, D with a well-developed chitinized arch following the end of the abdomen cuticle invagination.

DISTRIBUTION: Known only from the type locality (Bugaba, Panama) (fig. 5).

Cyrtognatha serrata Simon, 1897 Figures 60, 61

Cyrtognatha serrata Simon, 1897: 870.

TYPES: Nine syntypes from the St. Vincent Island, Saint Vincent, and the Grenadines, Lesser Antilles; no date or collector data on the label; 3 males, 2 females, and 4 juveniles (BMNH 1987.9.18.112; examined).

DIAGNOSIS: Although similar to *C. simoni* and *C. bryantae*, the male of *C. serrata* has a very characteristic apical apophysis of the conductor (fig. 60A, B). In *C. serrata* the conductor has two sharpened tips of almost the same size separated by a deep

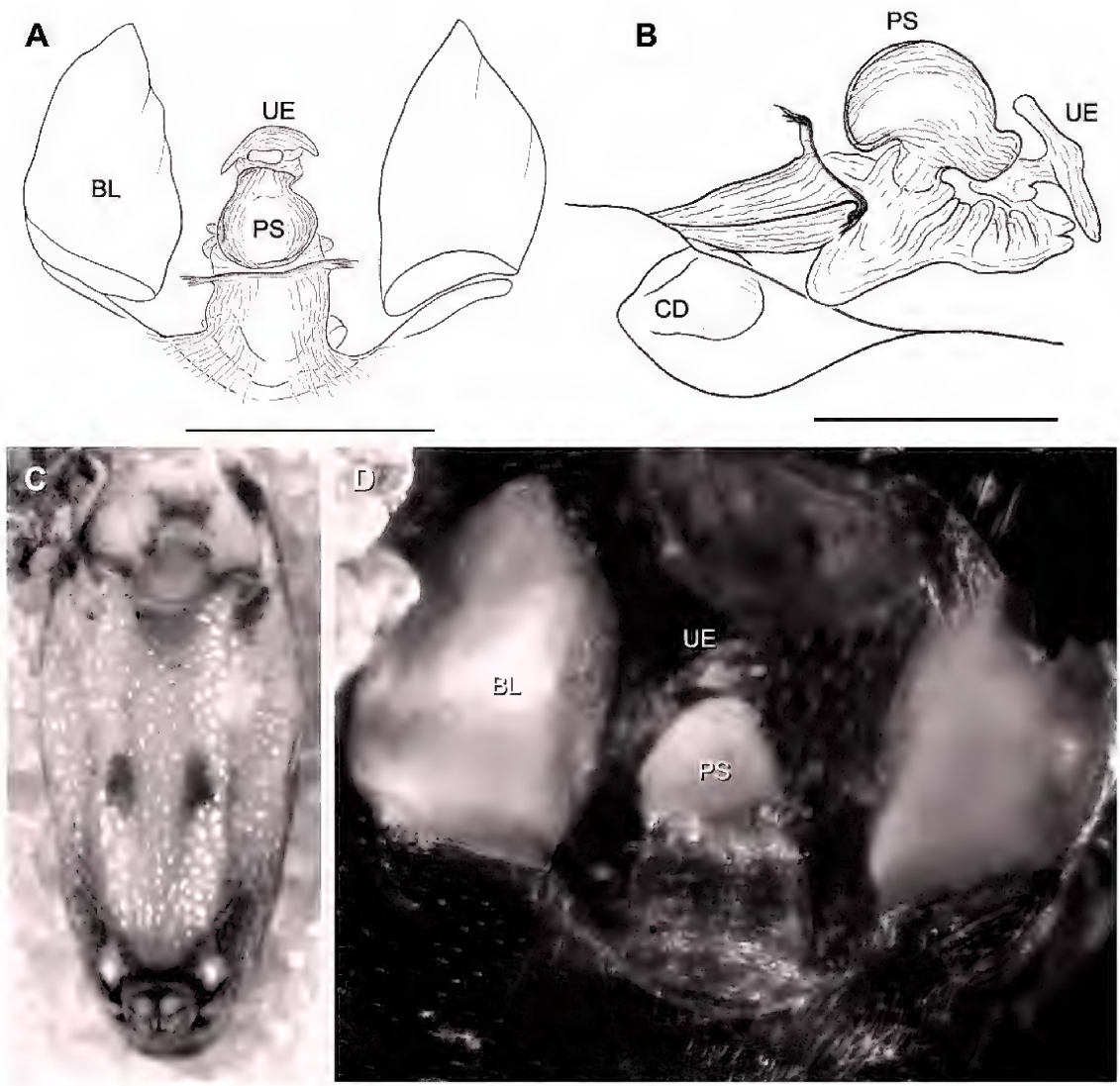

Fig. 59. *Cyrtognatha lepida*. Vulva: dorsal (A), lateral B. Female abdomen ventral C. Vulva dorsal (D). Scale bars A: 1 mm; B: 0.5 mm.

incision. In *C. serrata* the tip of the basal apophysis of the conductor is widened (in *C. simoni* and *C. bryantae* it is sharpened) and the embolus does not have the distal laminar fold observed in *C. bryantae* (fig. 52A, C). Males of *C. serrata* can be distinguished also by the shape of the paracymbium, which is wider and does not have the well-developed distal rounded widening observed in *C. bryantae* and *C. simoni*. Females are diagnosed by the small and cylindrically shaped chamber of the uterus externus (fig. 60D, E).

DESCRIPTION: *Male* (*syntype*). Habitus as in figure 61A–D. Carapace brown-yellowish, with a well-marked fovea, darker cephalic region, and darker coloration around the fovea. Abdomen elongated with gray-brownish color and numerous guanine spots, dorsally with two irregular longitudinal lines. Distally each line has a series of five darker markings, and the area between the lines is darker. Proximal and distal tubercles strongly reduced. Spinnerets as in most of the congeneric species are surrounded by darker pigmentation. Total length 4.52. Cephalotho-

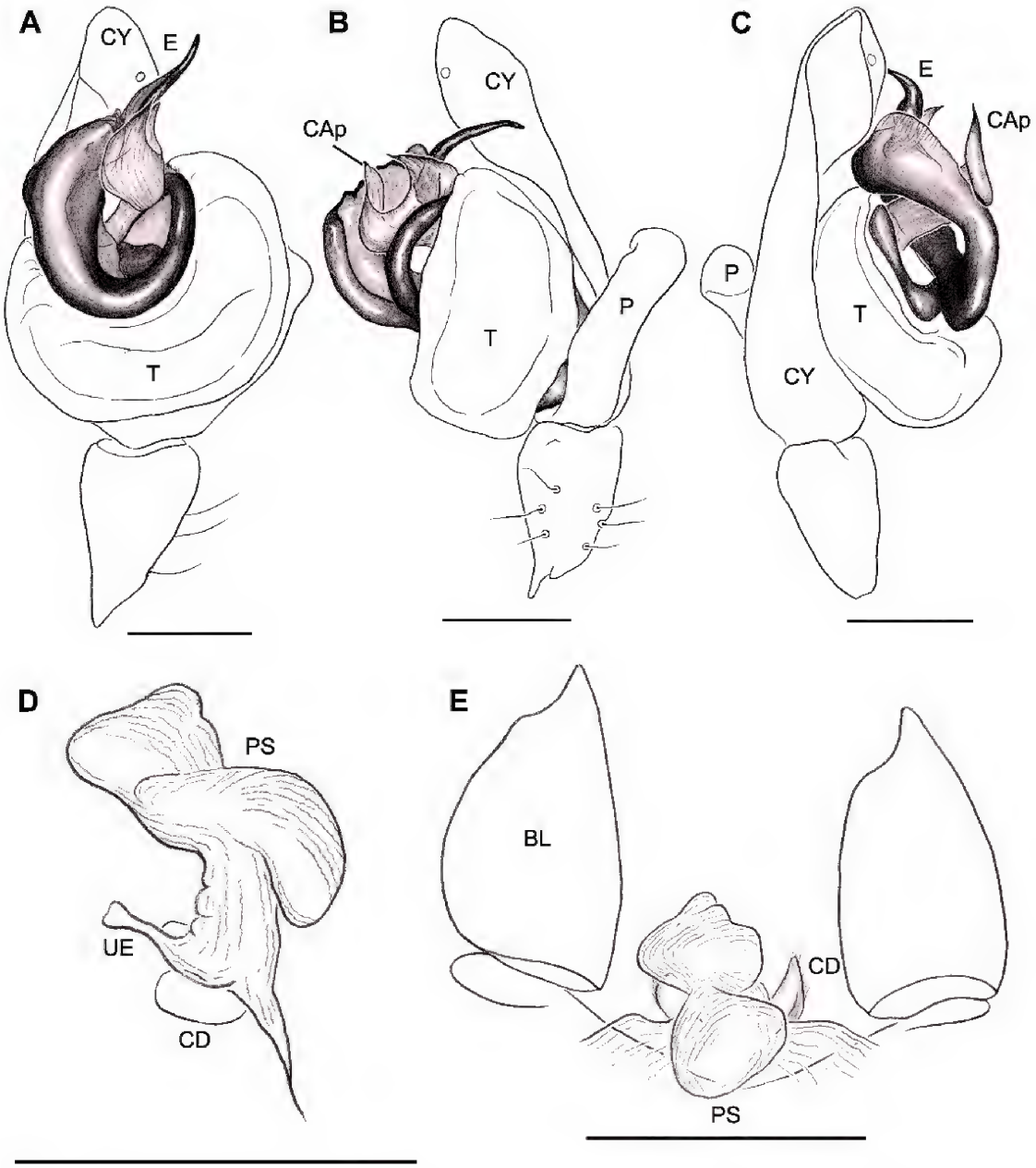

Fig. 60. *Cyrtognatha serrata*. Male palp: ventral (**A**), retrolateral (**B**), prolateral (**C**). Vulva: lateral (**D**), dorsal (**E**). Scale bars A–C: 0.2 mm; D, E: 0.5 mm.

rax 1.95 long, 1.27 wide, 0.87 high. Abdomen 2.57 long, 1.25 wide, 1.05 high. Sternum yellowish with brown colored labium and endites. Sternum 0.92 long, 0.90 wide. Chelicerae robust, dark brown, and moderately divergent. Cheliceral teeth very strong; dorsal tooth big, close to the fang articulation and curved prolaterally. Fangs very robust with well-developed outgrowth. Chelicerae as in figure 61B. Clypeus height 1.16 times one AME diameter. Eyes nearly the same size surrounded by darker pigmentation. Diameter of the AME 0.12. Distance between AME equal to their diameter; distance between

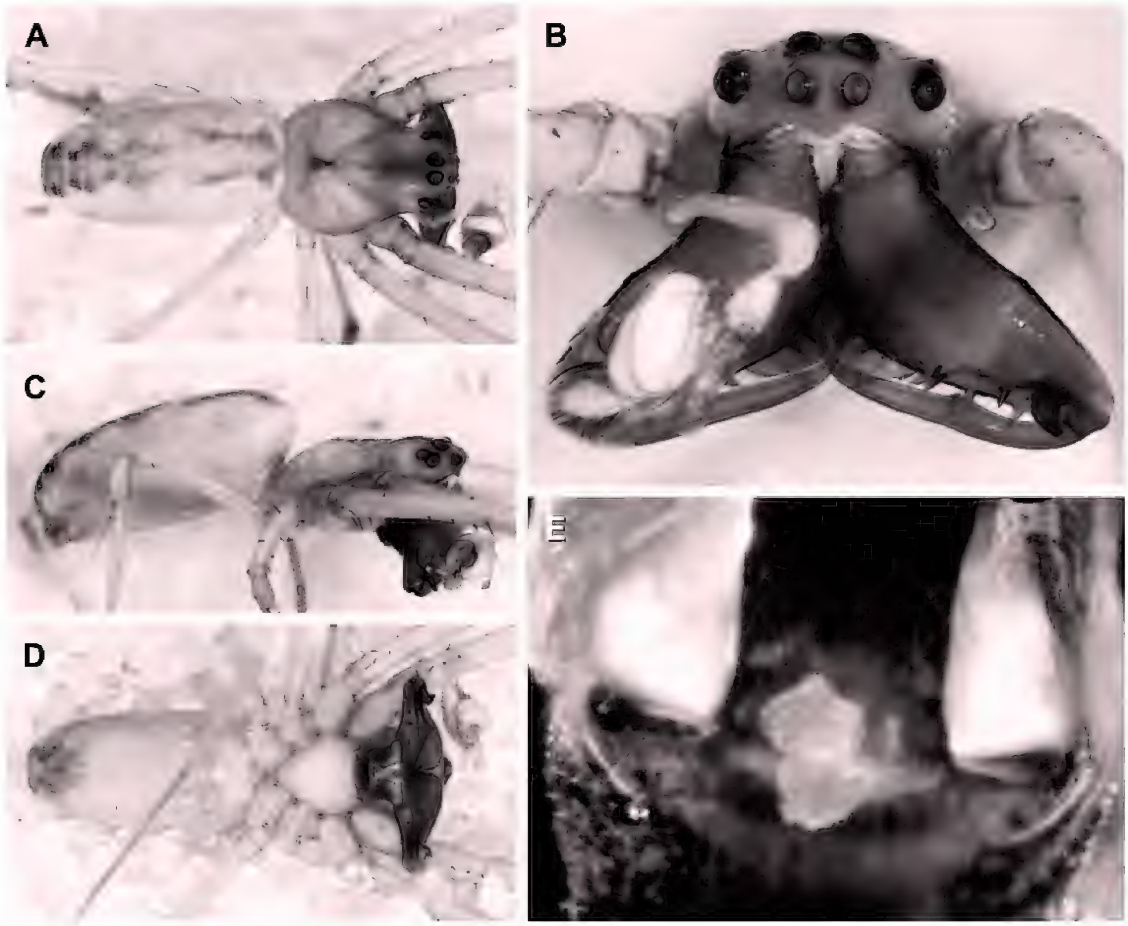

Fig. 61. *Cyrtognatha serrata*. Male habitus: dorsal (**A**), lateral (**C**), ventral (**D**). Male chelicerae (**B**). Vulva dorsal (**E**).

AME and ALE 1.5 AME diameters. Distance between PLE half of their diameter. Legs long with remains from greenish coloration. Femur I 3.87, 1.9 times the length of the cephalothorax. Pedipalp as in figure 60A–C. Palpal tibia length 0.28; cymbium length 0.70.

Female (*syntype*). Habitus and coloration as in the male except for the better developed proximal elevation of the abdomen. Eyes slightly closer to each other. Distance between AME less than their diameter. Distance between AME and ALE less than 1.5 AME diameters. Chelicerae not divergent and with coloration as the rest of the cephalothorax; only the fangs and the distal edges (including the cheliceral teeth) are darker. Dorsal tooth not developed. Total length 4.30. Cephalothorax 1.75 long, 1.25 wide, 0.87 high. Abdomen 2.55 long, 1.12 wide, 1.07 high. Sternum rounded, slightly longer than wide; 0.92 long, 0.90 wide. Clypeus height 0.53 times one AME diameter. AME diameter 0.10. Femur I 2.50, 1.4 times the length of the cephalothorax. Vulva as in figures 60D, E, 61E.

Variation. Cephalothorax length varies from 1.87 to 1.95 in males (n = 3) and from 1.75 to 2.05 in females (n = 2). Total body length in males varies from 4.52 to 4.49 (n = 3). The second female studied was missing the abdomen, and thus total length could not be calculated for this specimen.

DISTRIBUTION: This species is known only from St. Vincent Island in the Lesser Antilles (fig. 5).

Cyrtognatha nigrovittata Keyserling, 1881
Figures 62, 63

Cyrtognatha nigrovittata Keyserling, 1881: 276, pl. 11, fig. 5.

TYPE: Male holotype from Peru, Pumamarca. No date information on the label, K. Jelski and J. Sztolcman (MIZ 132; examined)

DIAGNOSIS: *Cyrtognatha nigrovittata* is diagnosed by the presence of a short claw-shaped apophysis on the metine embolic apophysis (fig. 62A, D). The membrane surrounding the distal part of the embolus (fig. 62A, B, D) is also very characteristic and different from all other *Cyrtognatha* species. The elongated abdomen with very long and longitudinally oriented distal tubercle is an additional diagnostic character that allows easy identification.

DESCRIPTION: *Male* (*holotype*). Habitus as in figures 62E, 63A–C. Carapace brownish with a well-marked fovea and darker median band. Legs brownish, darker than the cephalothorax. Abdomen cylindrical with brownish color and few remains of guanine spots. Proximal tubercles of the abdomen very small. Distal tubercle very large, conical, with the tip oriented caudally. The tubercle itself is almost as long as one-third of the abdomen (fig. 63B, C). Total length 7.80. Cephalothorax 2.41 long, 1.30 wide, 0.93 high. Abdomen 5.39 long, 0.93 wide, 0.93 high. Sternum yellowish with edges slightly darker with brownish pigmentation; 1.05 long, 0.93 wide. Endites and labium darker with brown pigmentation. Clypeus height 1.6 times one AME diameter. All eyes surrounded by darker pigmentation and nearly the same size. AME diameter 0.08. Distance between AME slightly larger than their diameter. Distance between AME and ALE 1.5 AME diameters. Distance between PLE equal to their diameter. ALE and PLE close to each other, placed over short elevations. Chelicerae (fig. 62E) widely divergent and darker than the rest of the cephalothorax. Dorsal cheliceral tooth very well developed and outlying the fang articulation. Cheliceral fang with a small outgrowth. Femur I 5.64, 2.3 times the length of the cephalothorax. Pedipalp as in figure 62A–D. Palpal tibia length 0.28; cymbium length 0.97.

Female. Unknown.

DISTRIBUTION: Known only from the type locality (fig. 5).

NOMEN DUBIUM

Cyrtognatha aproducta Franganillo, 1926 was originally described from Cuba. This species was omitted in Roewer's (1955) catalog, but it is included in Platnick's (2006) catalog with a small note about Roewer's decision. Franganillo's (1926) description does not provide diagnostic drawings and by itself is not sufficient to identify this species. Unfortunately, the collection of Pelegrín Franganillo has suffered serious damage through the years. It is currently deposited at the Instituto de Ecología y Sistemática in La Habana (Cuba) where recent examinations (Huber and Pérez González, 1998) found that many of the specimens are lost and the remaining material is not readily accessible because the vials lack labels. Huber and Pérez González (1998) noted that although the vials are numbered, the collection catalog has been lost so that the numbering does not provide any useful information.

Considering the current state of the Franganillo's collection and the insufficient information given in the original description, we consider *Cyrtognatha aproducta* to be a nomen dubium.

MISPLACED SPECIES

Genus *Tetragnatha* Latreille, 1804
Tetragnatha lactensis (Mello-Leitão, 1947), new combination
Figure 64

Agriognatha lactensis Mello-Leitão, 1947: 11, fig. 25

TYPE: Female holotype from Brazil, Minas Gerais, Carmo do Rio Claro, Jose C. M. Carvalho (MNRJ 1826; examined).

TRANSFER JUSTIFICATION: In the original description (Mello-Leitão, 1947) this specimen was placed in the genus *Agriognatha* without mentioning the most important female structure—the vulva—in Tetragnathinae, species that lack an epigynum. Detailed study of the internal female genitalia revealed

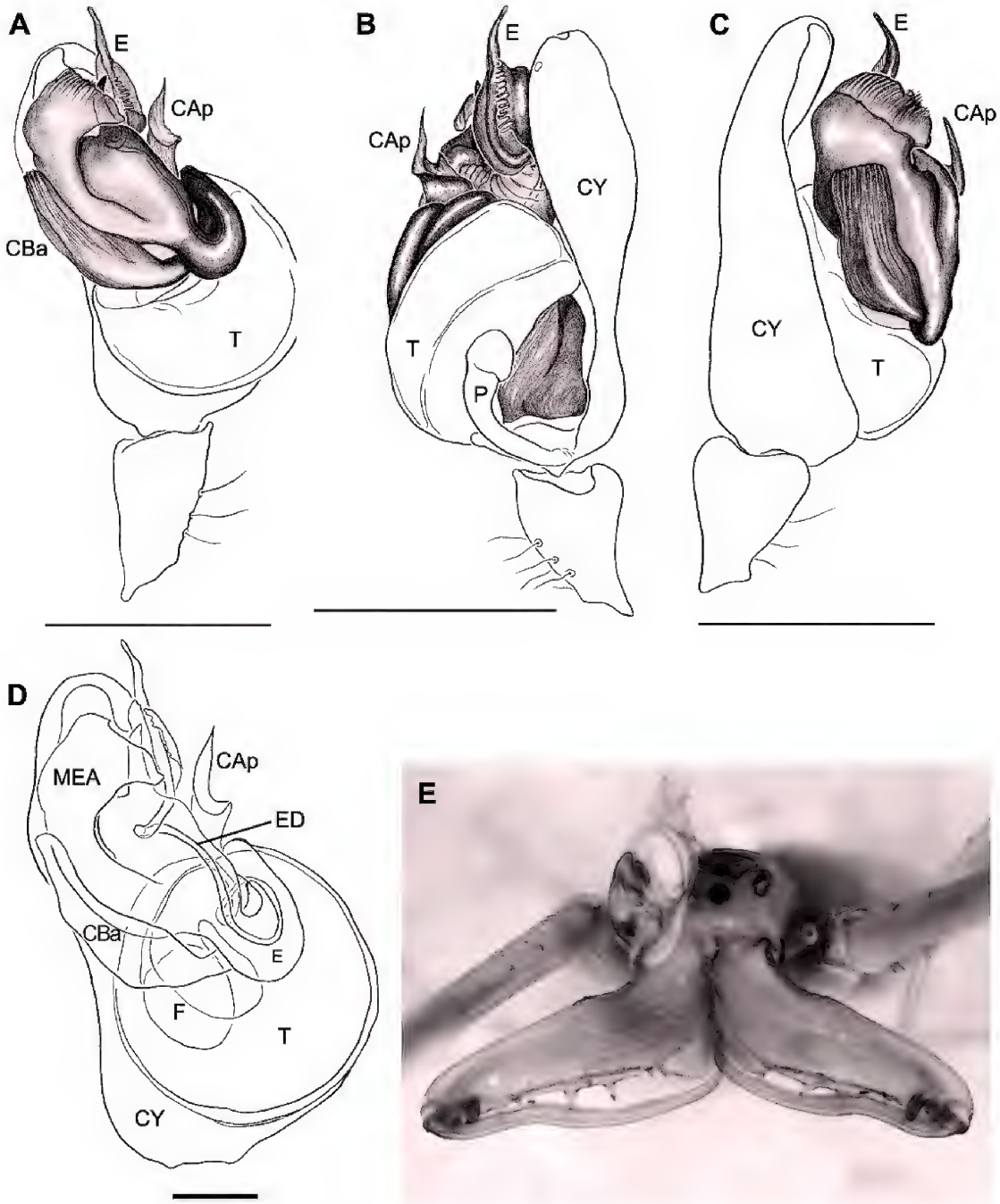

Fig. 62. *Cyrtognatha nigrovittata*. Male palp: ventral (**A**), retrolateral (**B**), prolateral (**C**). Male palp schematic: ventral (**D**). Male chelicerae (**E**). Scale bars A–C: 0.5 mm; D: 0.1 mm.

a bizarre morphology (fig. 64A, C, D), which does not exhibit the diagnostic characters of *Cyrtognatha*. Despite being so unusual, this morphology presents some characters common to all *Tetragnatha* species (e.g., small fingerlike posterior sac and spermathecae). Furthermore, the eye sizes and distribution, as well as the shape of the epigastric furrow

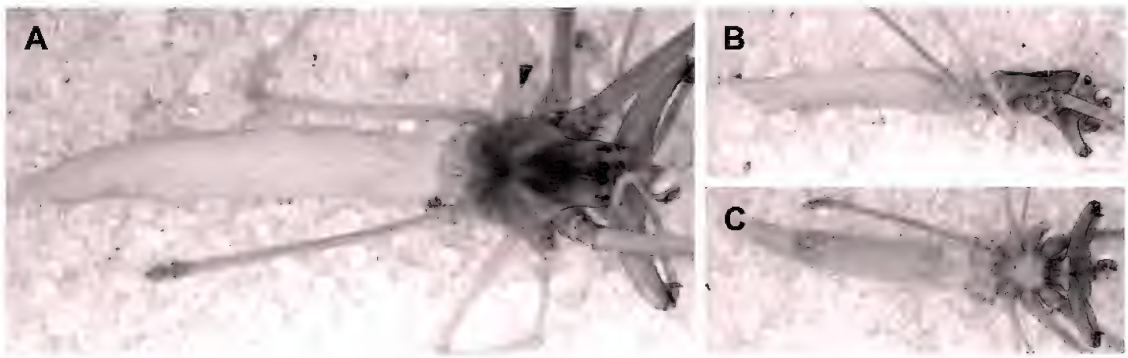

Fig. 63. *Cyrtognatha nigrovittata*. Male habitus: dorsal (**A**), lateral (**B**), ventral (**C**).

(fig. 64B), are as in *Tetragnatha*. Unfortunately, the male of this species remains unknown and there is only one female specimen available for study; thus, many important characters could not be examined. This complicates the decision about its correct placement; however, based on all the available evidence we consider it a member of the genus *Tetragnatha*.

DIAGNOSIS: This species can be easily distinguished from all known *Tetragnatha* by the very unusual shape of the spermathecae. Here the copulatory ducts are nearly straight and the spermathecae consist of a widened channel that is very tangled (fig. 64A, C, D) and narrows slightly toward its end.

DESCRIPTION: *Male*. Unknown.

Female (*holotype*). Carapace brownish, with dark brown pigmentation surrounding the eyes. Fovea well marked and placed roughly in the center of the thoracic region. Abdomen elongated with conical shape and brownish coloration. Distal edge of abdomen with darker markings dorsolaterally. Only very few guanine crystals remain (difficult to observe). Legs brown-yellowish. Femur of the fourth leg with short nonfeathered dorsal trichobothria. Total length 8.30. Cephalothorax 2.29 long, 1.55 wide, 1.05 high. Abdomen 6.01 long, 1.55 wide, 1.79 high. Sternum yellowish with darker margins; longer than wide; 1.17 long, 0.68 wide. Endites yellowish, rectangular, and wider distally. Labium slightingly darker than the sternum, trapezoidal, with swollen distal edge. Clypeus height 0.7 times one AME diameter. AME diameter 0.11. Eyes placed in two procurved rows; first row more procurve, second row nearly straight. PME larger than the other eyes. PLE and AME nearly the same diameter. ALE smallest (at about half of the PME diameter). Distance between AME 1.5 AME diameters; AME–ALE distance at about twice the AME diameter. AME–PME distance nearly the same as the distance between AME. PME slightly more separated than the AME. ALE and PLE close to each other but not juxtaposed; distance between ALE and PLE about 1.2 times one ALE diameter. Chelicerae yellowish, not divergent and without dorsal tooth. Femur I 4.96, 2.3 times the length of the cephalothorax. Vulva as in figure 64A, C, D. Epigastric furrow as in figure 64B.

DISTRIBUTION: Known only from the type locality in Minas Gerais (Brazil).

Tetragnatha exilima (Mello-Leitão, 1943), new combination
Figure 65

Cyrtognatha exilima Mello-Leitão, 1943: 176.
Cyrtognatha exilima Brignoli, 1983: 221.

TYPE: Female holotype in Brazil, Rio Grande do Sul, P. Ramos (MNRJ 41757; examined)

TRANSFER JUSTIFICATION: After examining the type specimen we consider the placement of this species in *Cyrtognatha* to be incorrect, as it lacks any of the diagnostic characters of this genus (e.g., PLS macrosetae, feathered trichobothria of femur IV, touching PLE, reduction of the spermathecae). It has the eye pattern, genital morphology (fig. 65A, B), and shape of the endites

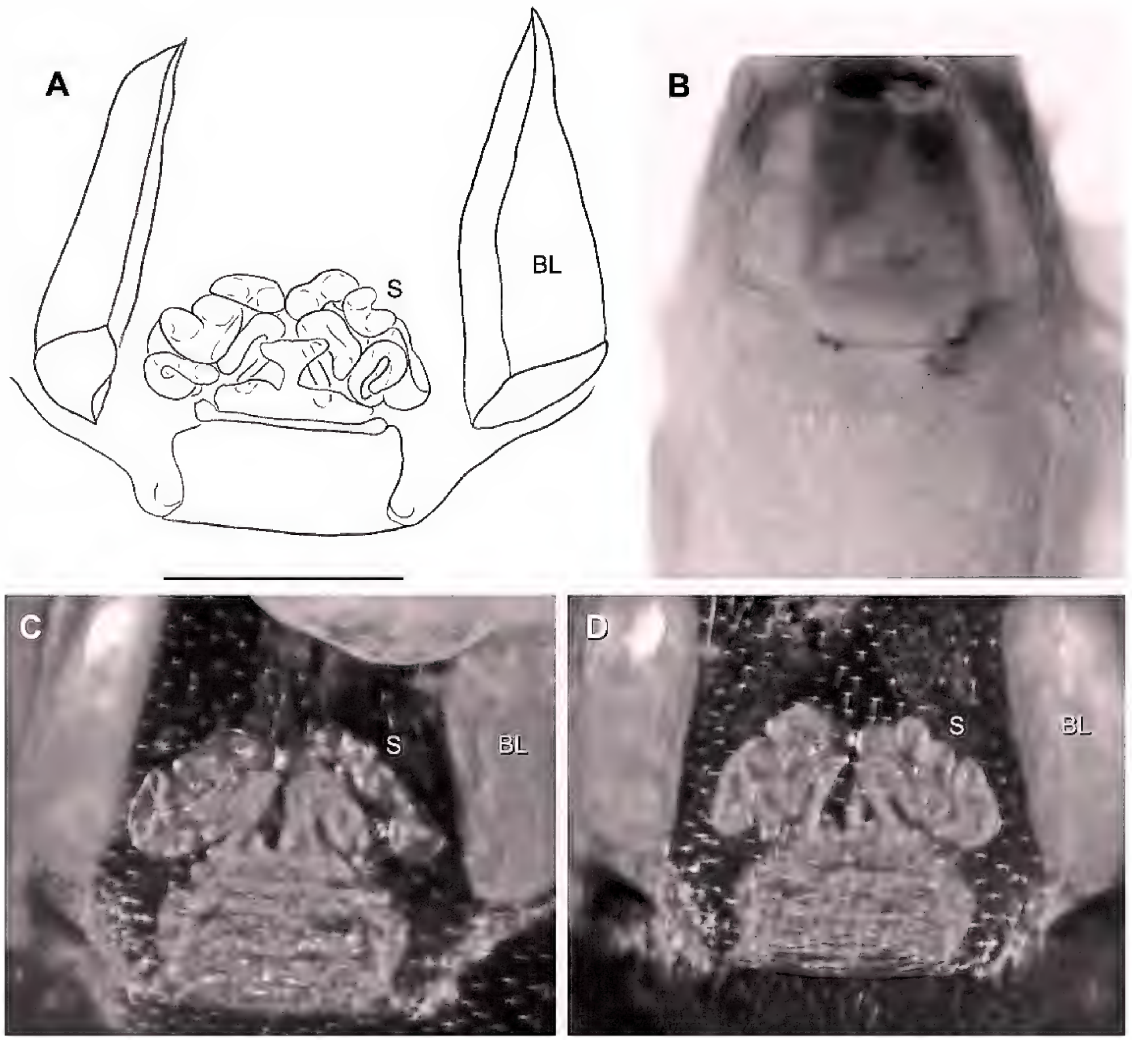

Fig. 64. *Tetragnatha lactensis*. Female vulva: dorsal (**A**). Female epigastric furrow (**B**). Female vulva: dorsal (**C**), ventral (**D**). Scale bar 0.5 mm.

and labium (fig. 65E) as in *Tetragnatha*, and therefore it is transferred to the latter genus.

DIAGNOSIS: The shape of the spermathecae and the morphology and placement of the uterus externus (fig. 65A) are diagnostic. Although the spermathecae in this specimen are not completely chitinized, they can be easily observed and allow clear distinction of this species from other congeners.

DESCRIPTION: *Male*. Unknown.

Female (*holotype*). Habitus as in figure 65B–E. Carapace brown-yellowish, elongated, and centrally with a well-marked fovea. Cephalothorax width very uniform except for the slightly narrower cephalic region. Abdomen cylindrical, very long with numerous guanine spots dorsally. The guanine spots extend over the upper half of the lateral sides of the abdomen. The remains of the lateral surface of the abdomen and its ventral part lack guanine crystals and exhibit a darker brownish pigmentation. Total length 6.84. Cephalothorax 1.57 long, 0.75 wide, 0.50 high. Abdomen 5.27 long, 0.75 wide, 0.75 high. Sternum yellowish, longer than wide, 0.87 long, 0.50 wide. Endites divergent and wider distally. Labium with swollen distal edge. Clypeus height 3.4 times one AME diameter. AME diameter 0.06. Eyes in two procurved rows. Anterior eyes

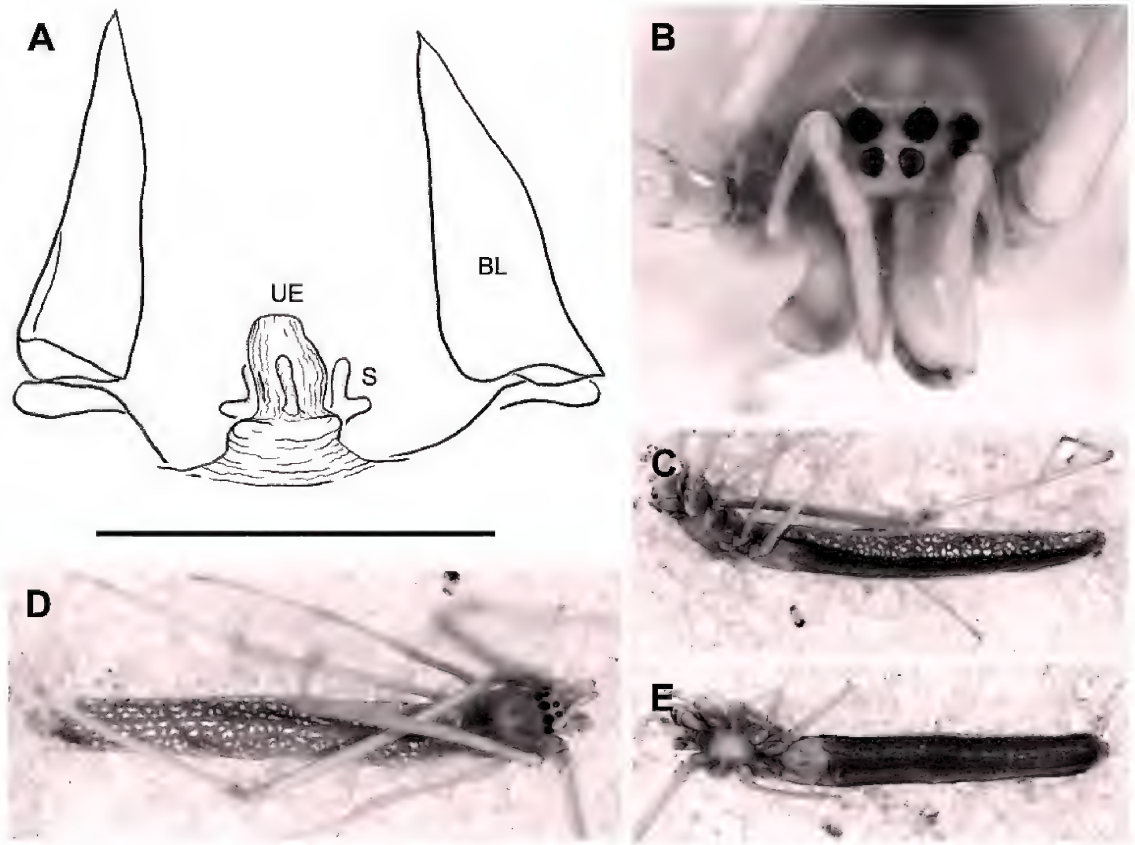

Fig. 65. *Tetragnatha exilima*. Female vulva: dorsal (**A**). Female chelicerae: frontal (**B**). Female habitus: lateral (**C**), dorsal (**D**), ventral (**E**). Scale bar 0.5 mm.

smaller than the posterior. ALE smallest and placed close to the PLE. Distance between AME 2.5 times one AME diameter; AME–ALE distance 1.5 times one AME diameter. PLE and PME nearly the same size. Distance between PME equal to their diameter; PLE–PME distance about 1.5 PLE diameters. All eyes are surrounded by an area with dark brown pigmentation. Chelicerae (fig. 65B) yellowish with seven anterior and two posterior teeth. One of the anterior teeth away from the other six almost in the middle of the distal margin of the chelicerae. The other six close to each other, placed on the retrolateral margin and with gradually increasing size distally. Femur I 4.96, 3.1 times the length of the cephalothorax. Vulva as in figure 65A.

DISTRIBUTION: Known only from the type locality in Rio Grande do Sul (Brazil).

Genus *Glenognatha* Simon, 1887

Glenognatha globosa (Petrunkevitch, 1925), new combination

Figure 66

Cyrtognatha globosa Petrunkevitch, 1925: 123, fig. 42.

TYPE: Female holotype from Panama, San Lorenzo. 4.xii.1924, A. and W. Petrunkevitch (most likely subadult), holotype (YPM; examined).

TRANSFER JUSTIFICATION: Detailed study of the holotype of this species showed that it has all of the diagnostic characters of the genus *Glenognatha*. The chelicerae are shaped as in *Glenognatha*, and the cheliceral teeth are also as in this genus (fig. 66D, E). The abdomen is globular and does not have a distal tubercle, while in *Cyrtognatha* it is oval to cylindrical and usually has a distal

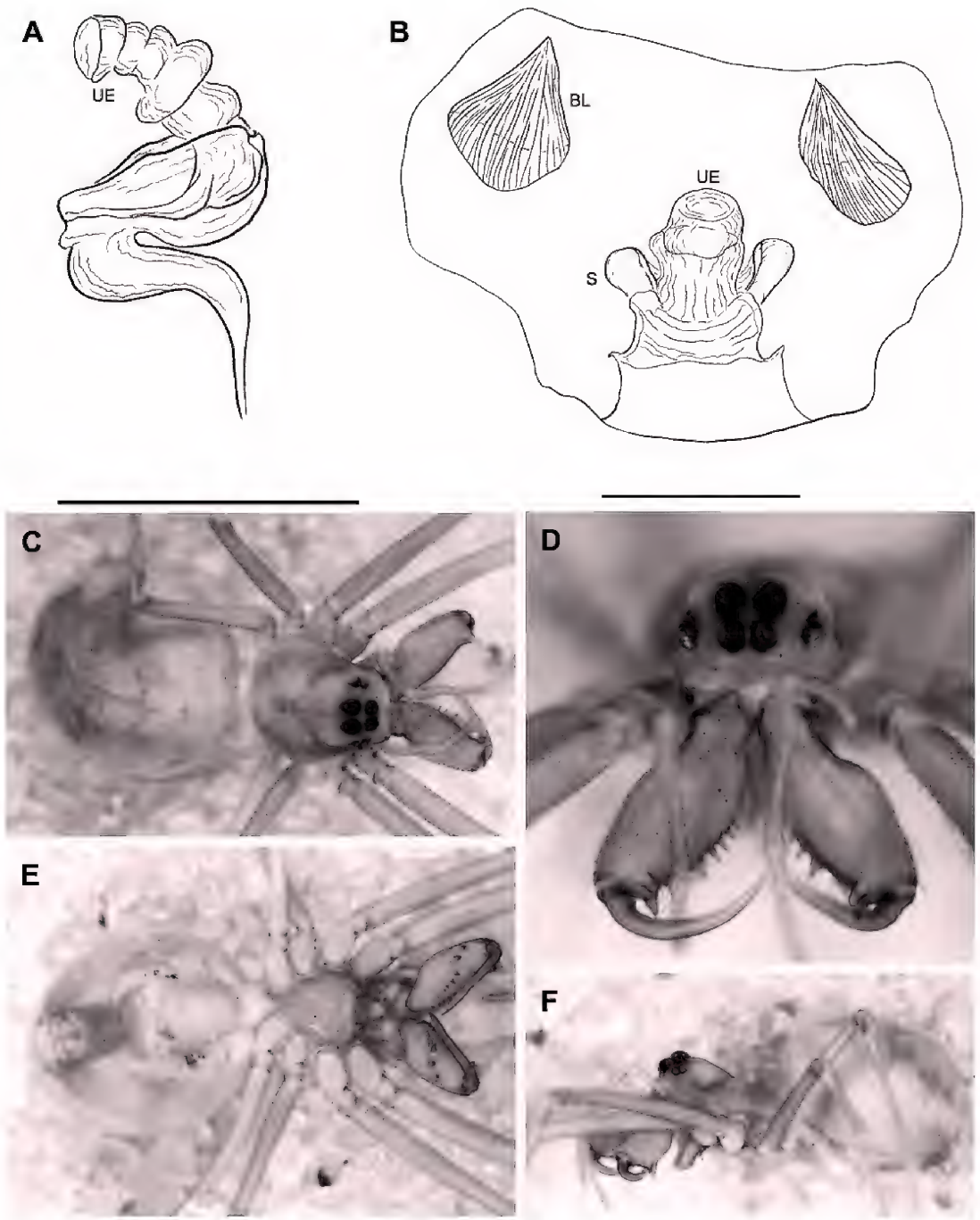

Fig. 66. *Glenognatha globosa*. Female vulva: lateral (**A**), dorsal (**B**). Female habitus: dorsal (**C**), ventral (**E**), lateral (**F**). Female chelicerae frontal (**D**). Scale bars 0.5 mm.

tubercle. Femur IV lacks the feathered trichobothria that occur in *Cyrtognatha*. The single most important character suggesting the placement of this specimen in *Glenognatha* is the advanced tracheal spiracle, a unique characteristic of *Glenognatha* and one of the most robust autapomorphies of this genus. Based on all these findings we

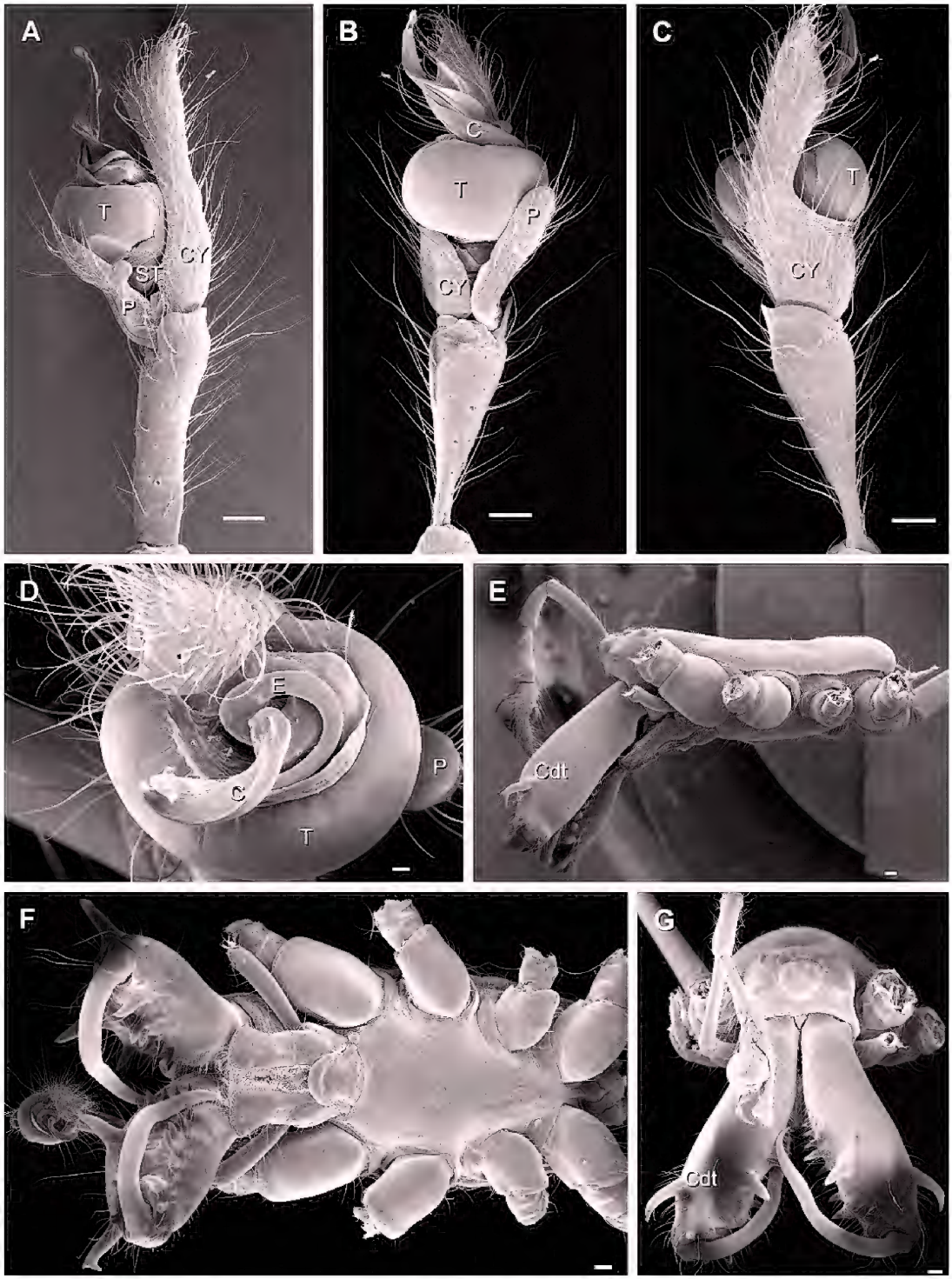

Fig. 67. *Tetragnatha javana*. Male palp: retrolateral (**A**), ventral (**B**), dorsal (**C**), apical (**D**). Male cephalothorax: lateral (**E**), ventral (**F**). Male chelicerae (**G**). Scale bars A–C, E–G: 100 μm; D: 20 μm.

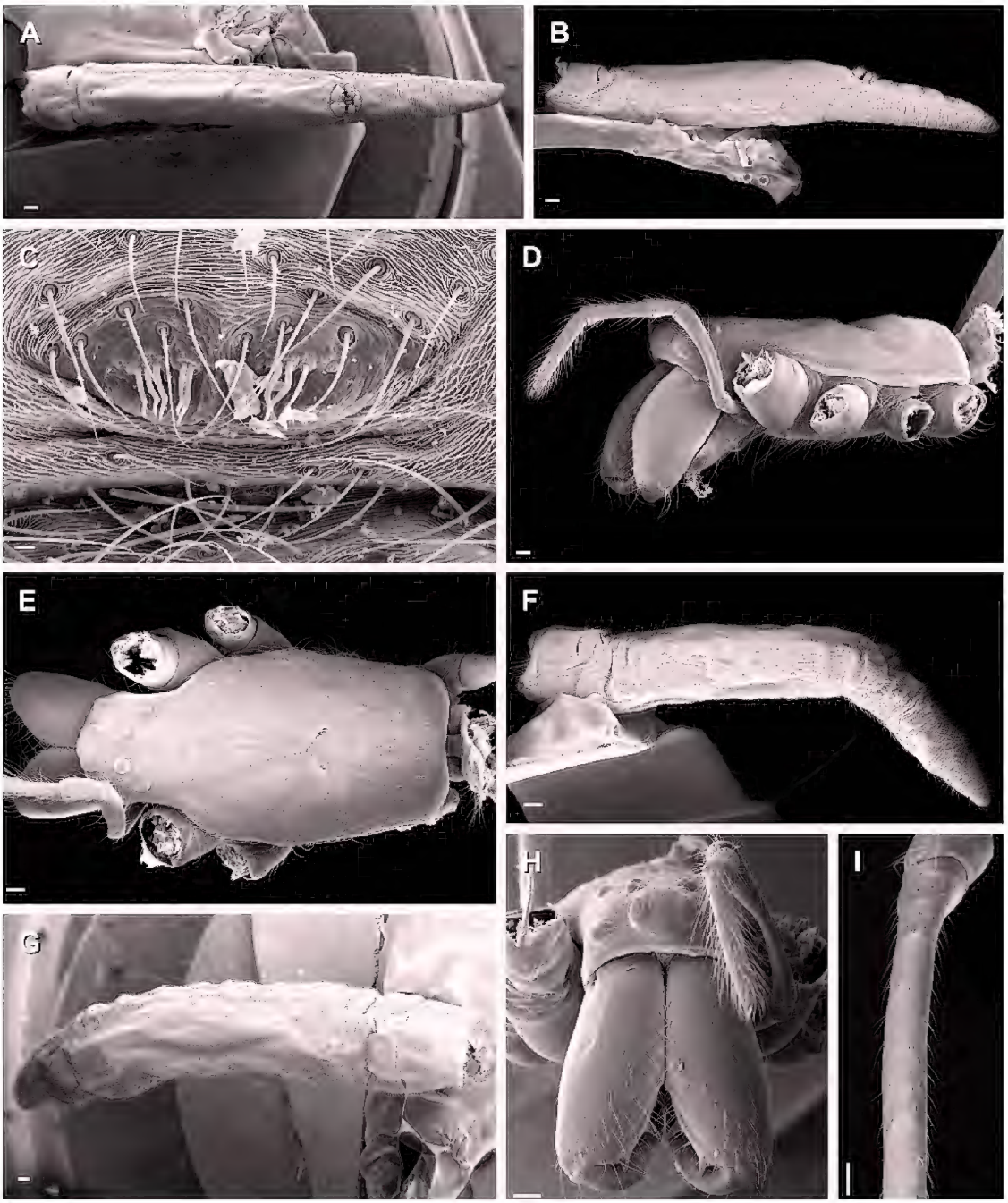

Fig. 68. *Tetragnatha javana*. Male abdomen: ventral (**A**), lateral (**B**). Epiandrous fusules (**C**). Female cephalothorax: lateral (**D**), ventral (**E**). Female abdomen: lateral (**F**), ventral (**G**). Female chelicerae: frontal (**H**). Female leg IV femur (**I**). Scale bars A, B, F: 200 μm; C: 10 μm; D, E, G, H, I: 100 μm.

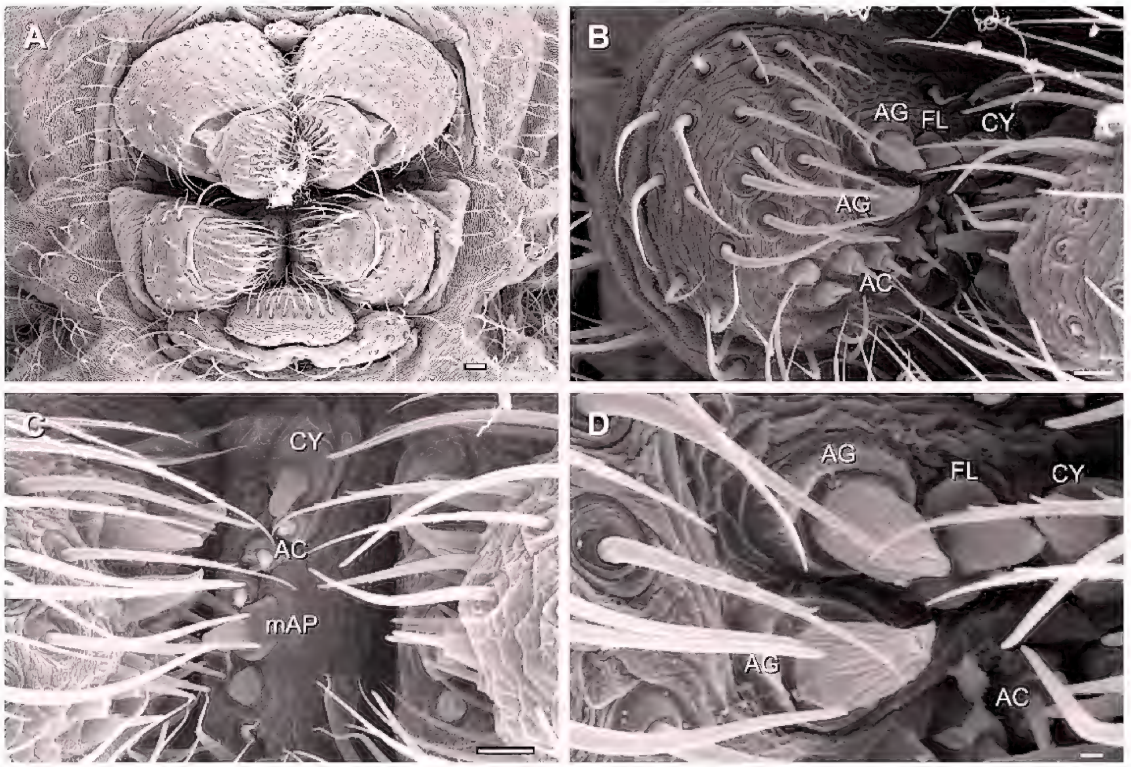

Fig. 69. *Tetragnatha javana*. Female spinnerets: ventral (**A**). Female PLS (**B**). Female PMS (**C**). Female PLS: close look (**D**). Scale bars A: 20 μm; B, C: 10 μm; D: 2 μm.

consider that the transfer of this species to *Glenognatha* is fully justified.

DIAGNOSIS: The specimen depicted in figure 66A, B is most probably a subadult female, and thus the spermathecae are not completely formed. However, the morphology of the uterus externus and the median membranous chamber of the vulva (fig. 66A,B) are very different from those observed in other *Glenognatha* species. The presence of a series of widened rings on the chamber connecting with the uterus externus (fig. 66A, B) is unique to this species.

DESCRIPTION: *Male*. Unknown.

Female (*holotype*). Habitus as in figure 66C–F. Carapace yellow-brownish with a well-marked fovea. Cephalic region elevated with easily distinguishable cephalic junction. Abdomen spherical with remains of distinctive marking dorsally and darker band ventrally (this specimen is very depigmented and it is impossible to say what its coloration pattern is when alive). Total length 3.99. Cephalothorax 1.62 long, 1.25 wide, 1.00 high. Abdomen 2.37 long, 2.12 wide, 1.75 high. Sternum yellowish, slightly darker than the rest of the cephalothorax; 0.75 long, 0.80 wide. Endites slightly wider distally and almost parallel. Labium trapezoidal, elongated, and with darker basal part. Clypeus height 1.7 times one AME diameter. AME diameter 0.12. Eyes in two rows, anterior row procurved, posterior row almost straight. Lateral eyes smaller and very close to each other (touching in their bases). Median eyes grouped close together frontally. AME slightingly smaller than PME. Distance between AME half of their diameter; AME–ALE distance twice one AME diameter. Distance between PME equal to their diameter and between them and PLE 1.5 PLE diameters. All eyes surrounded by a darker pigmentation. Chelicerae (fig. 66D) robust, narrower proximally, and with two rows (one anterior and one posterior) of strong teeth distally. Each row has eight teeth

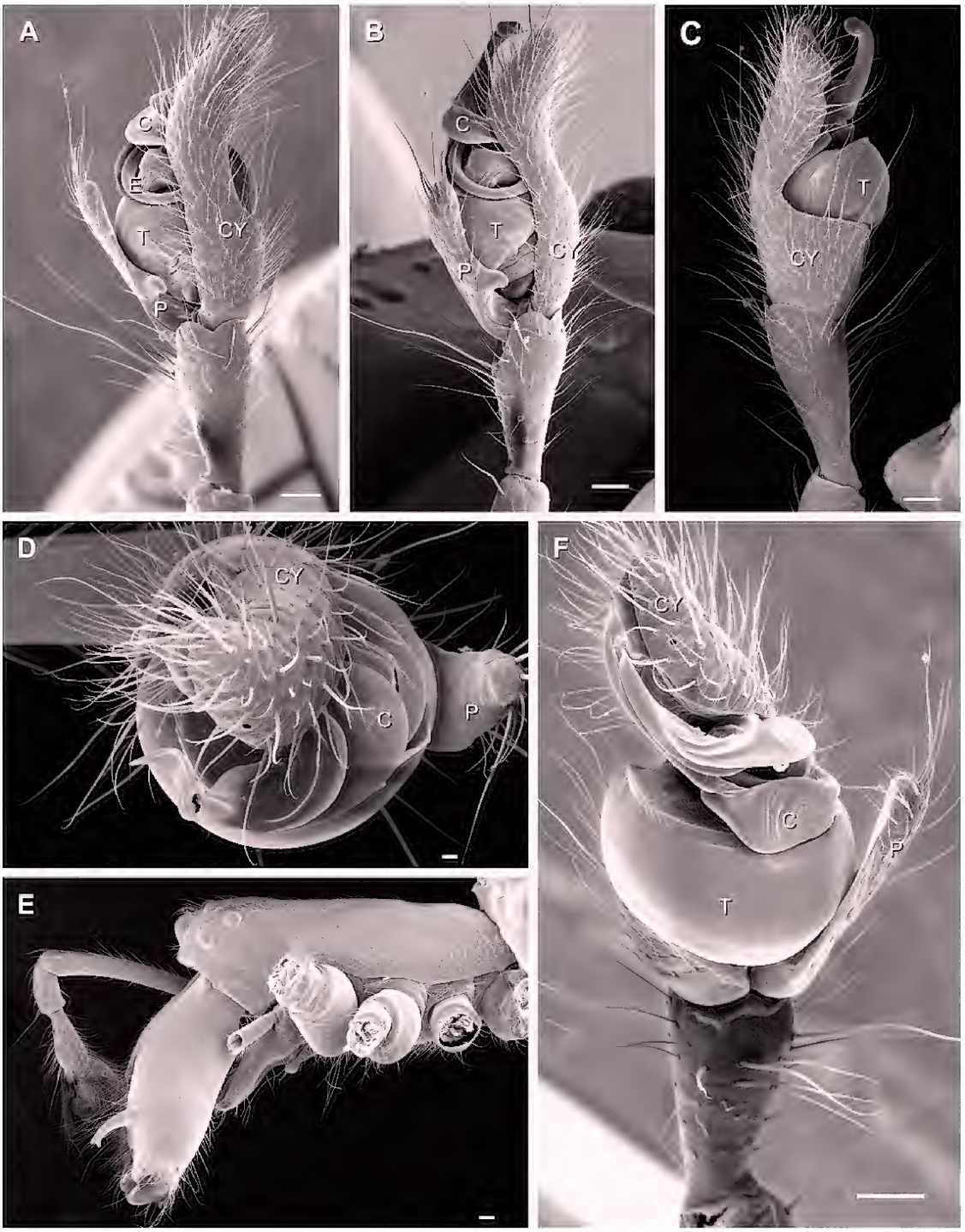

Fig. 70. *Tetragnatha* sp. from Dominican Republic. Male palp: dorsoretrolateral (**A**), retrolateral (**B**), prolateral (**C**), apical (**D**), ventral (**F**). Male cephalothorax lateral (**E**). Scale bars A–C, E, F: 100 μm; D: 20 μm.

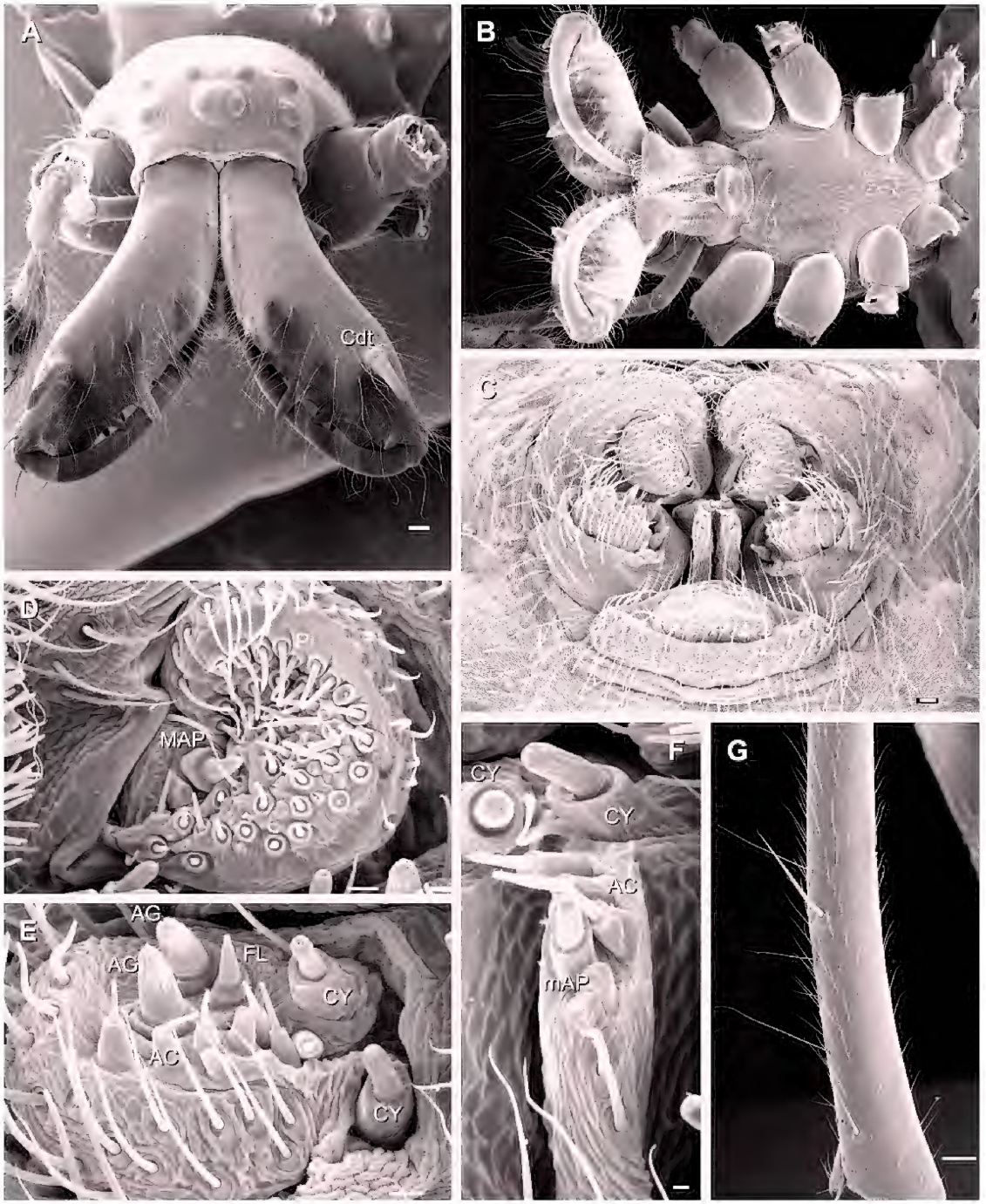

Fig. 71. *Tetragnatha* sp. from Dominican Republic. Male chelicerae: frontal (**A**). Male cephalothorax: ventral (**B**). Female spinnerets: ventral (**C**). Female ALS (**D**). Female PLS (**E**). Female PMS (**F**). Female leg IV femur (**G**). Scale bars A, B, G: 100 μm; C: 20 μm; D, E: 10 μm; F: 3 μm.

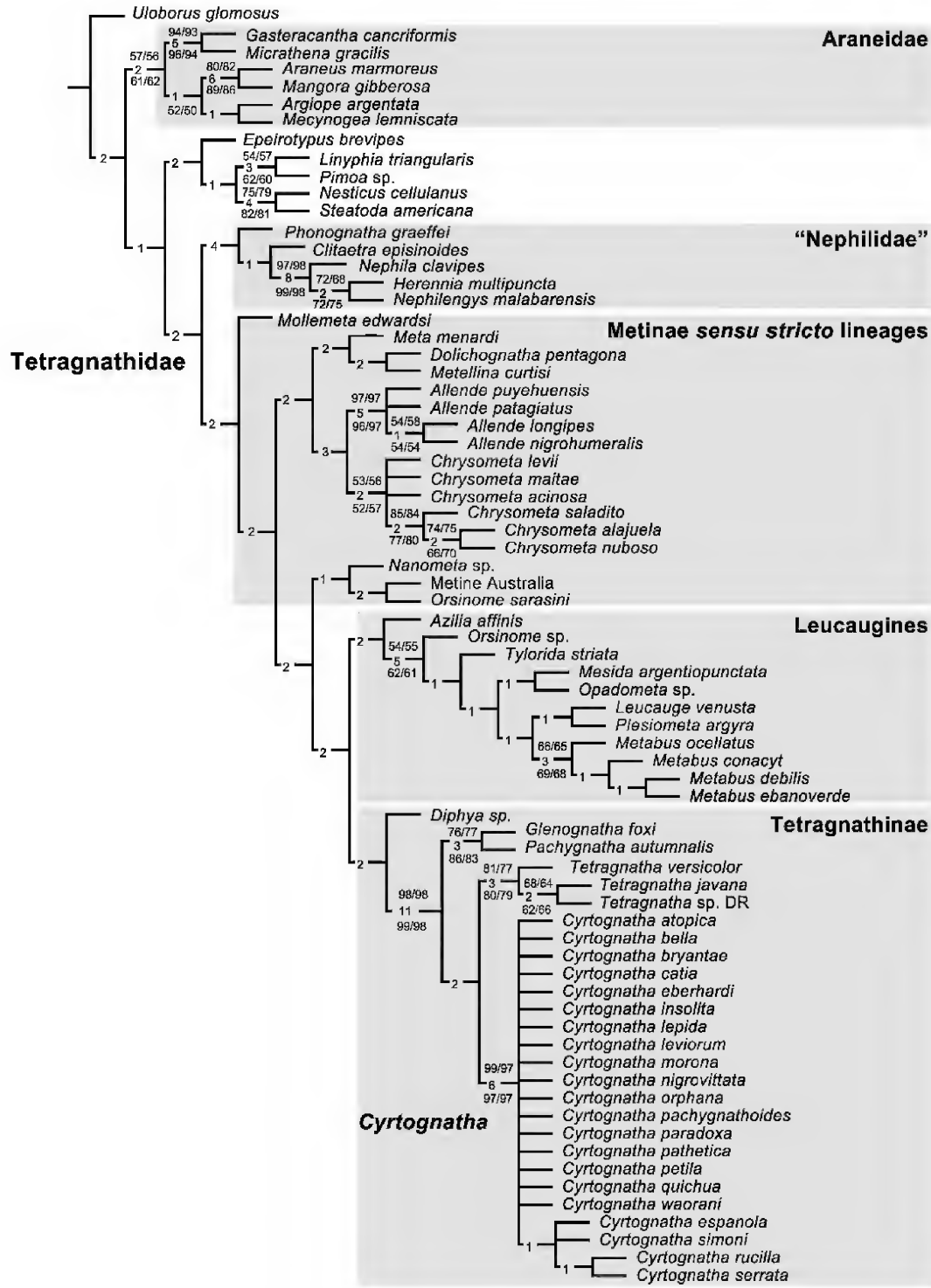

Fig. 72. Strict consensus of the 74 trees found by TNT analyzing the complete matrix under the equal weights parsimony criterion. L = 767 steps; CI = 32.2; RI = 71.8. Numbers cutting the branches represent the Bremer support; over the branches, standard bootstrap/Poisson bootstrap; below the branches, jackknife/symmetric resampling.

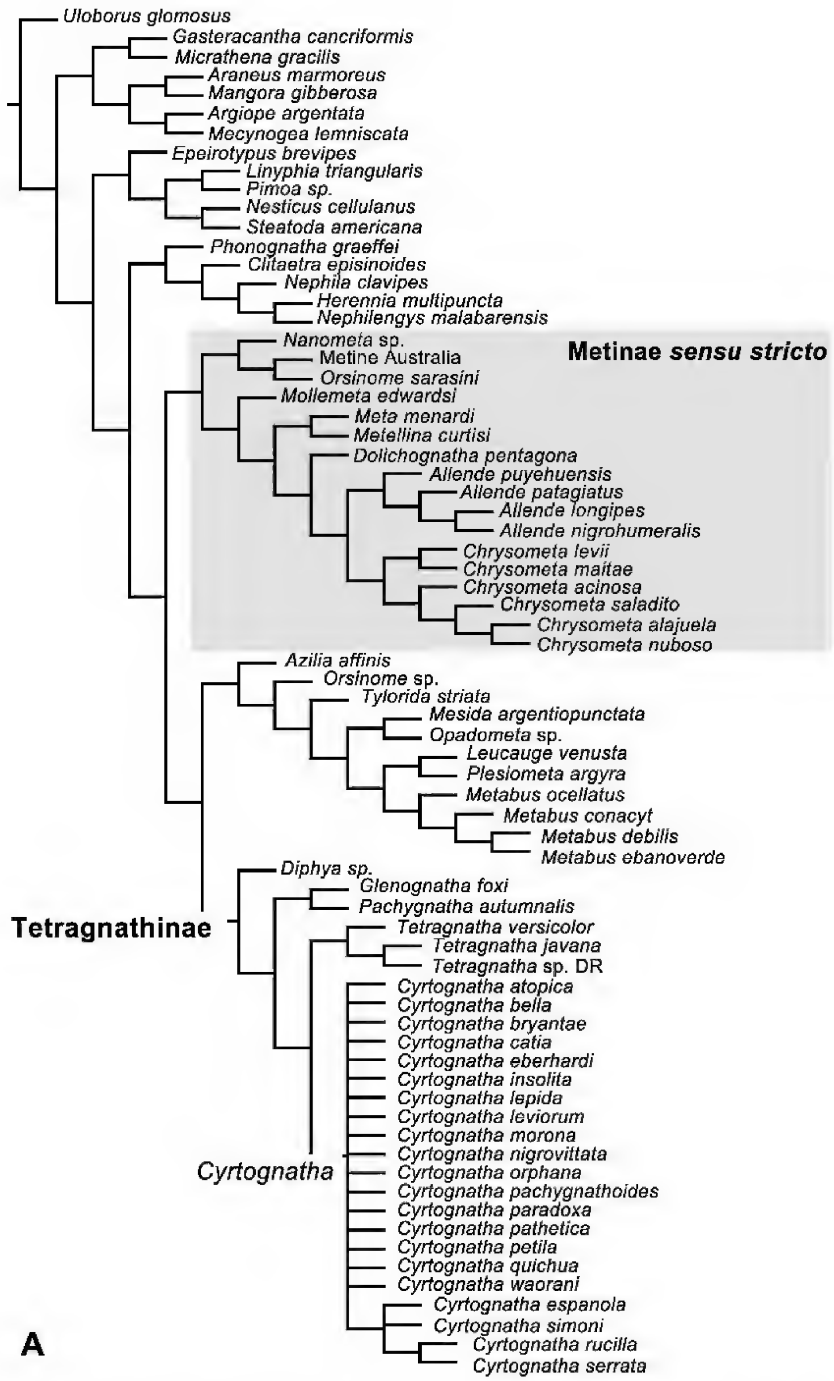

Fig. 73. A. Strict consensus of 94 trees found under the successive weighting criterion analyzing the complete matrix. L = 768 steps; CI = 32; RI = 71. B. Strict consensus of the 40 trees found by TNT under equal weights parsimony criterion analyzing the matrix m_noCh_noPat. The numbers cutting the branches represent the Bremer support.

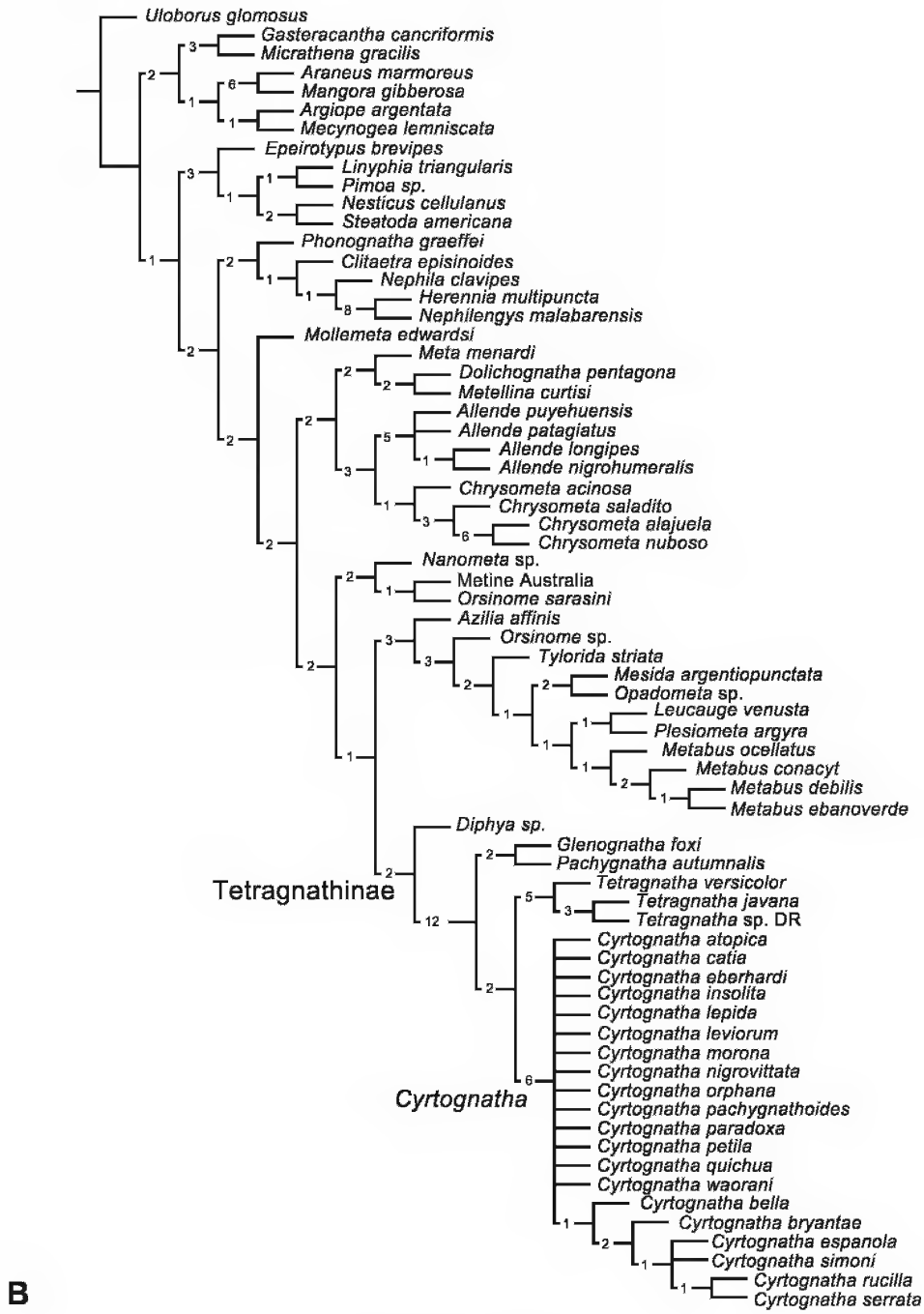

Fig. 73. Continued.

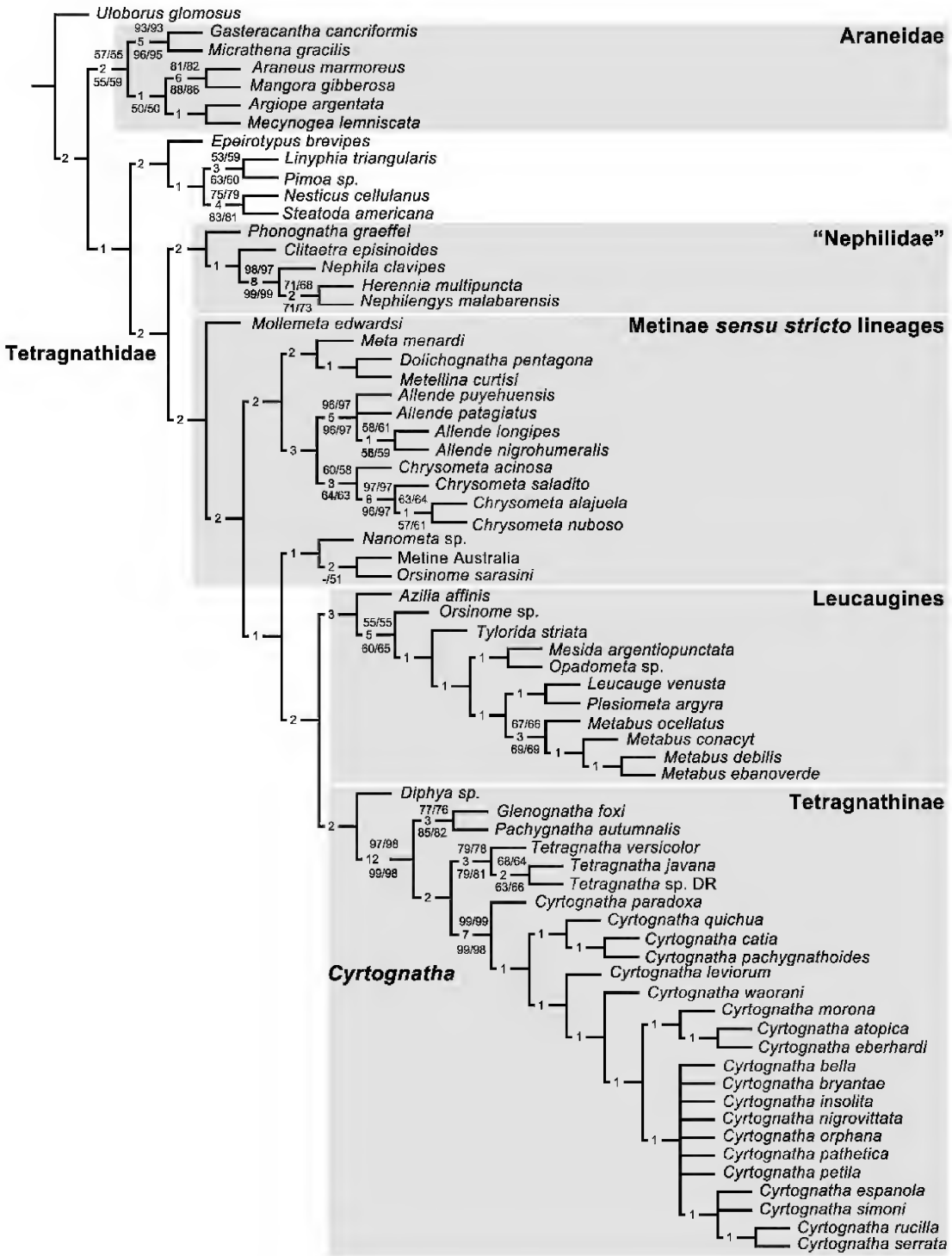

Fig. 74. Strict consensus of the six trees found by TNT under the equal weights parsimony criterion analyzing the matrix m_noCh_noLep. L = 731 steps; CI = 33.8; RI = 72. Numbers cutting the branches represent the Bremer support; over the branches, standard bootstrap/Poisson bootstrap; below the branches, jackknife/symmetric resampling.

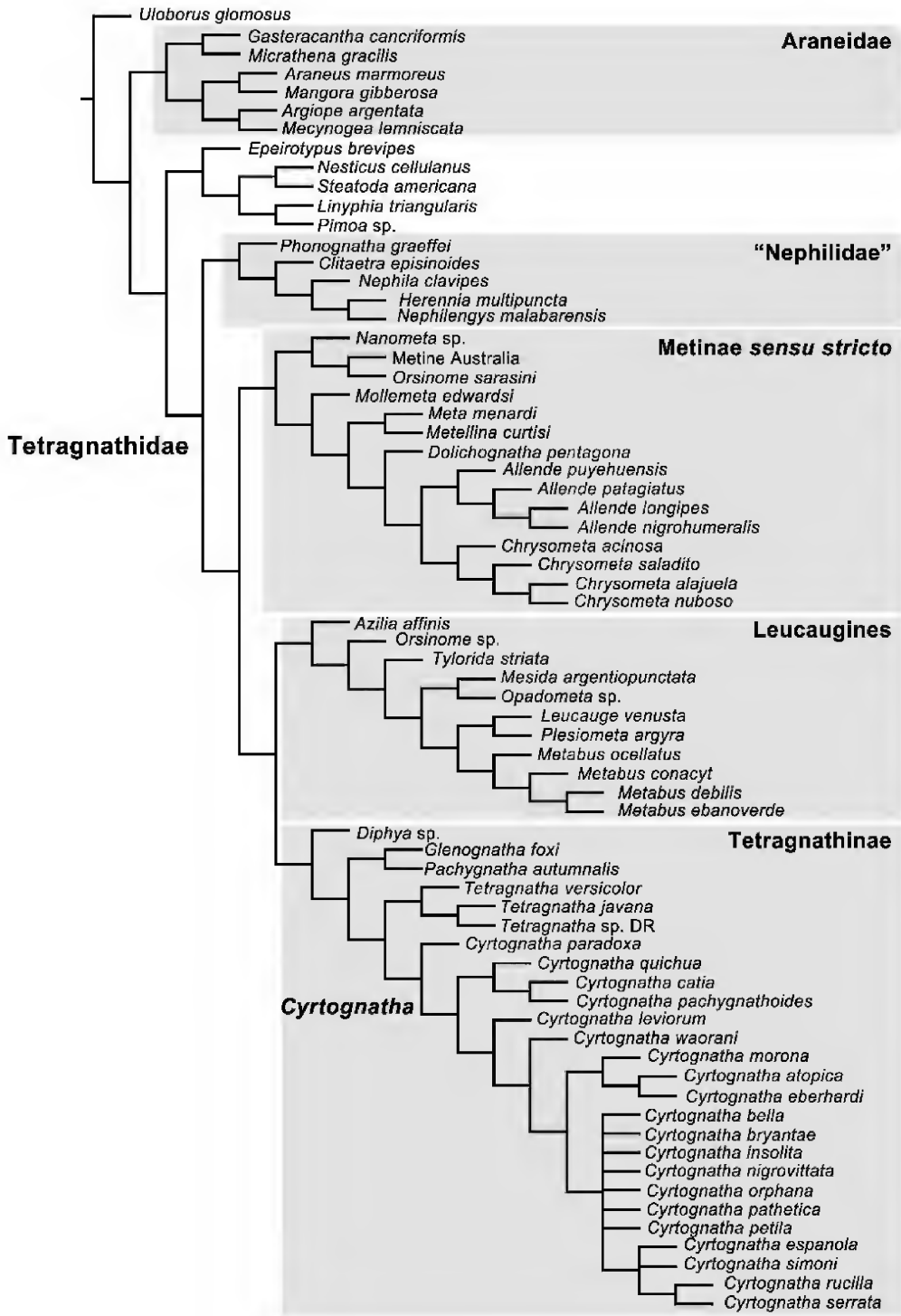

Fig. 75. Strict consensus of four trees found under the successive weighting criterion analyzing the matrix m_noCh_noLep. L = 734 steps; CI = 33; RI = 73.

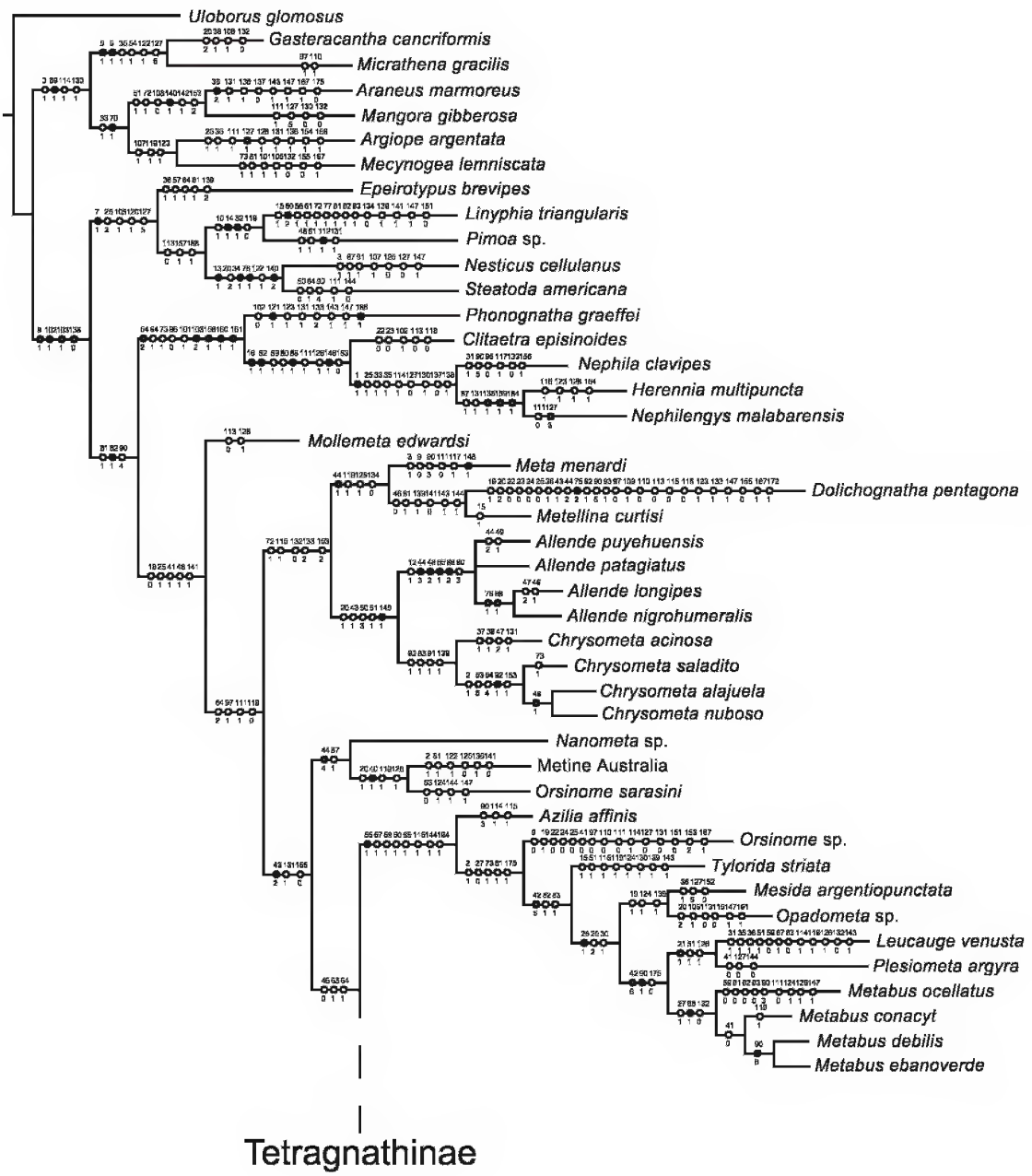

Fig. 76. Strict consensus of the two trees found by TNT under the equal weights parsimony criterion analyzing the matrix m_noCh_noLepPat. L = 719 steps; CI = 34.4; RI = 74.4. Filled circles represent unique (nonhomoplasious) gains or reversals; open circles represent homoplasious character changes. Character numbers are placed over the branches and the states are shown below the branches.

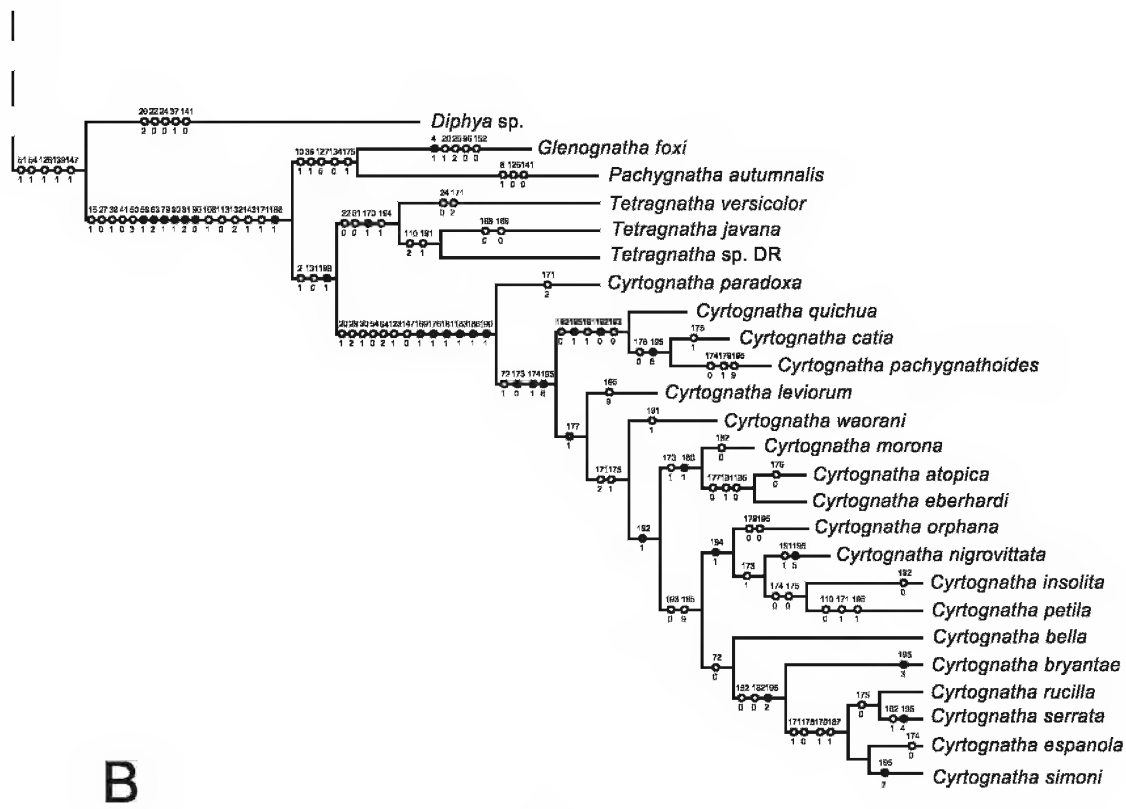

Fig. 76. Continued.

increasing in size toward the fang. Dorsal tooth present, well developed, and outlying the fang articulation. Femur I 2.75, 1.7 times the length of the cephalothorax. Vulva as in figure 66A, B.

DISTRIBUTION: Known only from the type locality in Panama.

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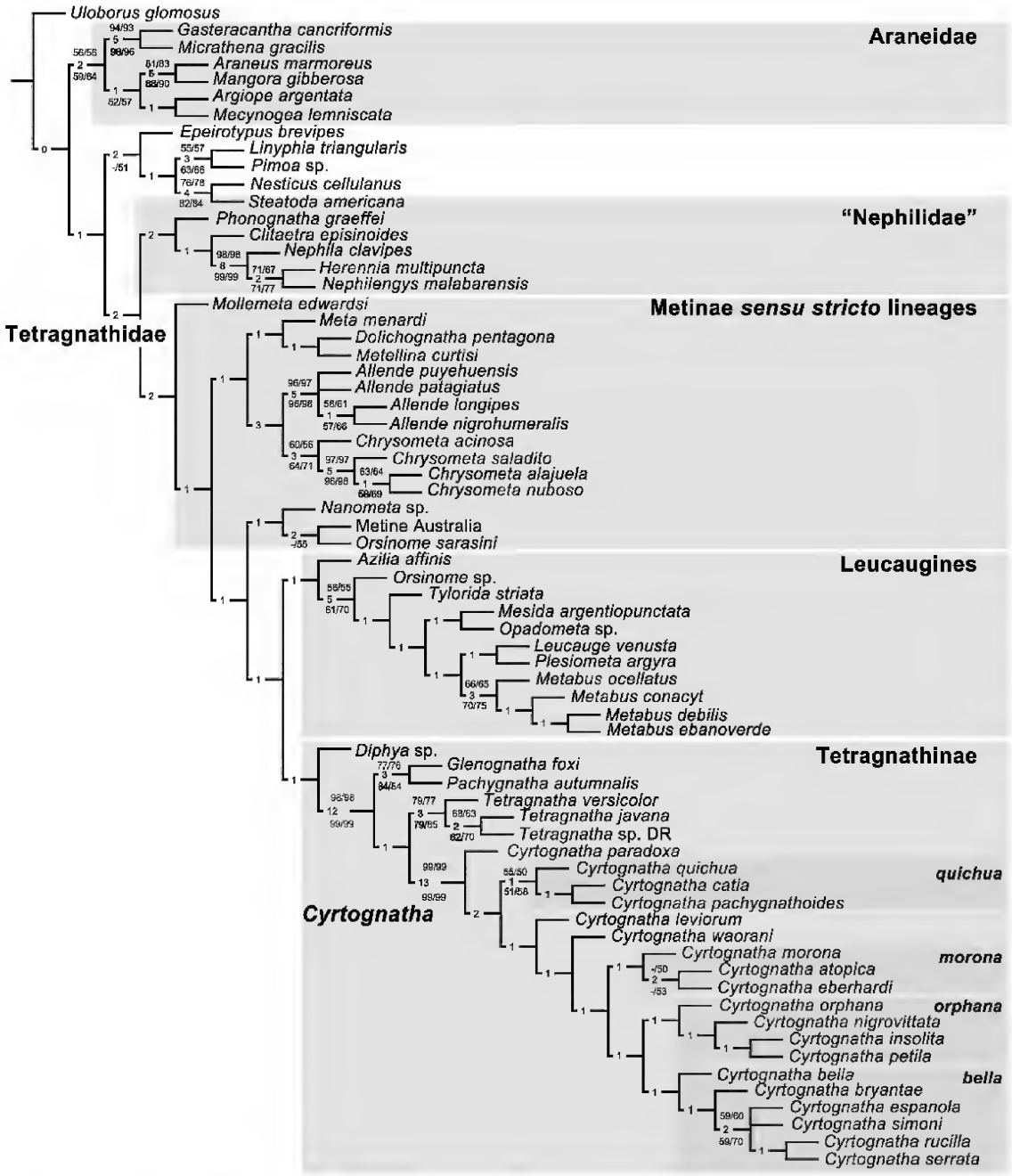

Fig. 77. Strict consensus of the two trees found by TNT under the equal weights parsimony criterion analyzing the matrix m_noCh_noLepPat. L = 719 steps; CI = 34.4; RI = 74.4. Numbers cutting the branches represent the Bremer support; over the branches, standard bootstrap/Poisson bootstrap; below the branches, jackknife/symmetric resampling.

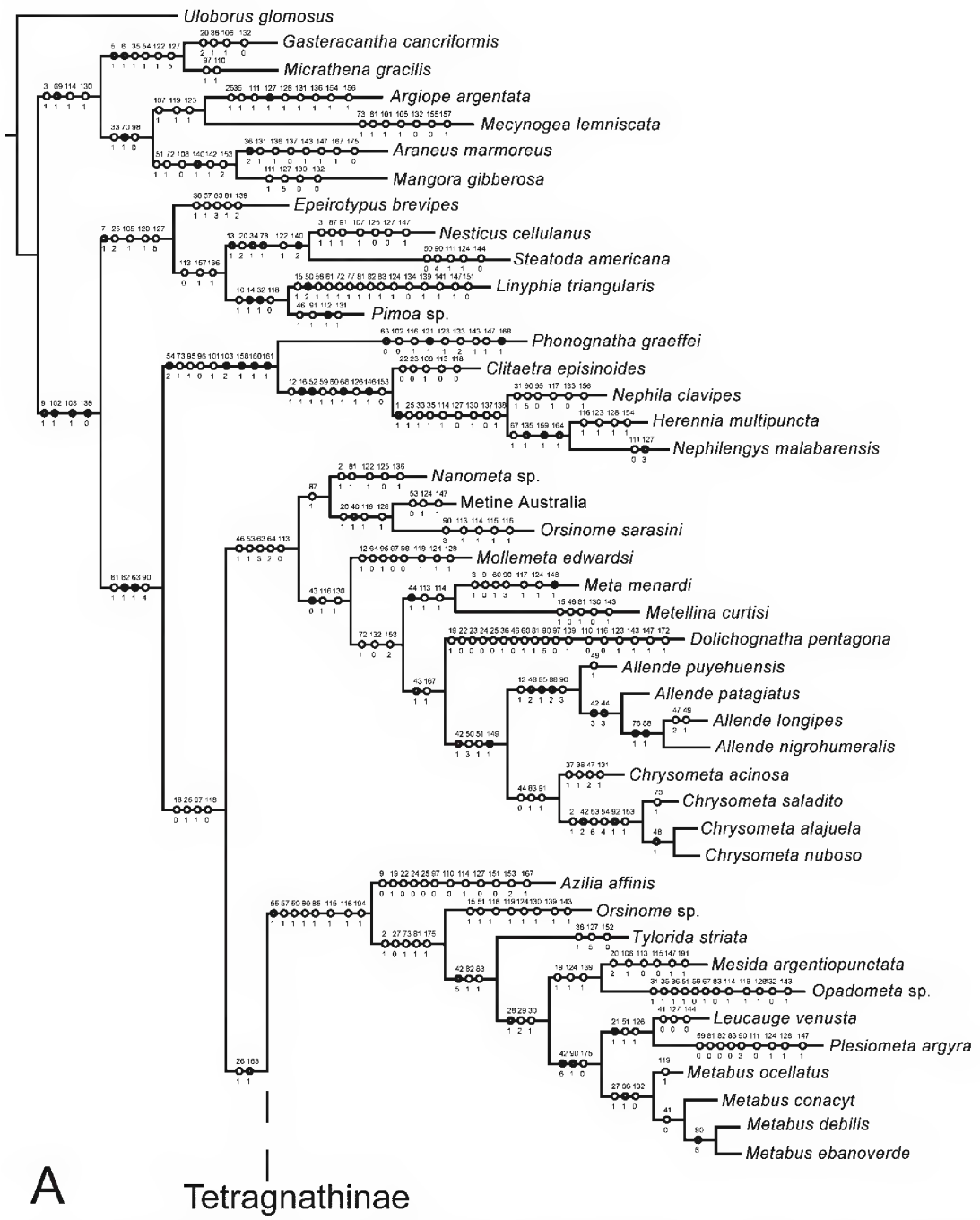

Fig. 78. The unique most parsimonious tree found under the successive weighting criterion analyzing the matrix m_noCh_noLepPat. L=722 steps; CI = 34; RI = 74. Filled circles represent unique (nonhomoplasious) gains or reversals; open circles represent homoplasious character changes. Character numbers are placed over the branches and the states are shown below the branches.

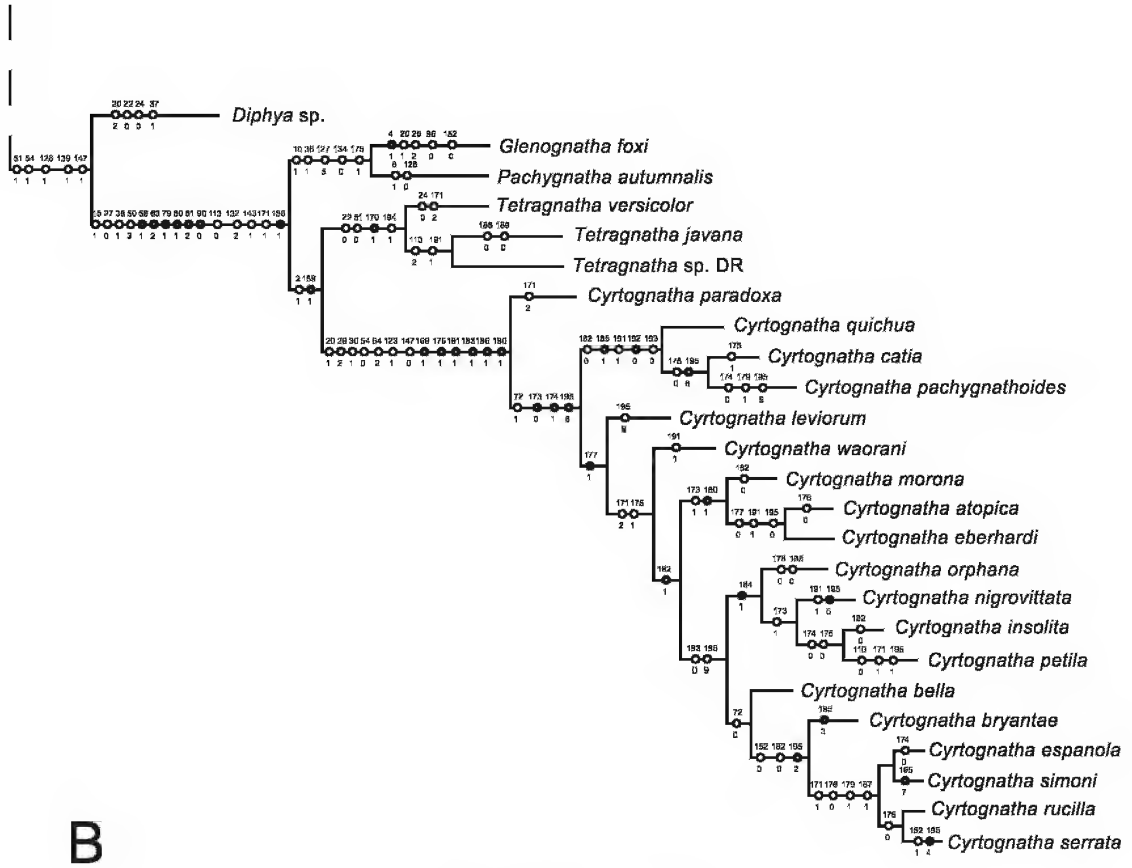

Fig. 78. Continued.

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Fig. 79. Alternative topologies obtained analyzing the matrix m_noCh_noLepPat under the implied weighting criterion. **A**. When K varies between 1 and 3 (depicted $K = 2$). **B**. When $K = 9$–20 (depicted $K = 10$). **C**. When $K > 20$ (depicted $K = 25$).

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Fig. 79. Continued.

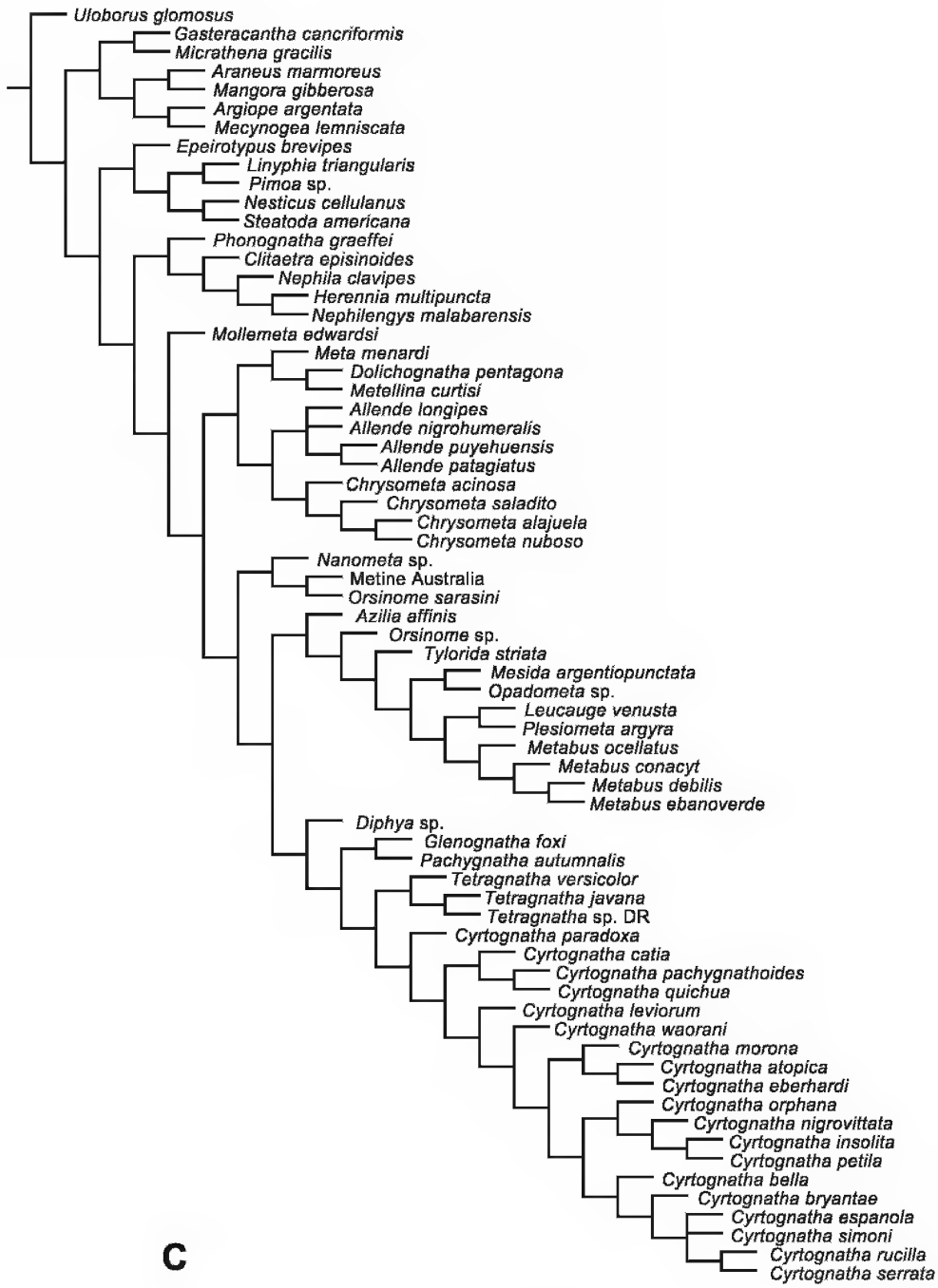

Fig. 79. Continued.

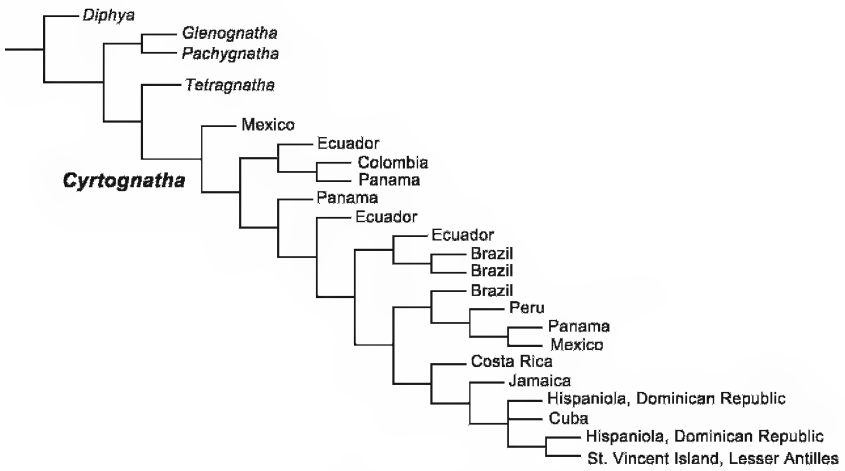

Fig. 80. Area cladogram of the *Cyrtognatha* species based on the strict consensus of the two most parsimonious trees found under equal weights analyzing the matrix m_noCh_noLepPat.

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APPENDIX 1

Character Descriptions

Characters that have been used in previous cladistic analyses are listed together with references. Many of the characters describing the web building behavior, which were widely used in previous studies and are also present here, were originally described by Eberhard (1982, 1990). Some of the characters were described long ago and have been widely used in spider taxonomy. In such cases we have generally given an example only of the more recent usage, and thus citation does not necessary imply authorship.

1. Male dorsal scutum: (0) absent; (1) present (Hormiga et al., 1995; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
2. Abdominal dorsal surface: (0) without guanine silver patches; (1) with guanine silver patches (Tanikawa, 2001; Álvarez-Padilla, 2007).
3. Booklung cover: (0) smooth; (1) grooved (Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Tanikawa, 2001; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
4. Tracheal spiracle: (0) posterior; (1) advanced (Hormiga et al., 1995; Álvarez-Padilla, 2007).
5. Gasteracanthinae abdominal spines: (0) absent; (1) present (Scharff and Coddington, 1997; Álvarez-Padilla, 2007).
6. Sclerotized ring around spinnerets: (0) absent; (1) present (Scharff and Coddington, 1997; Álvarez-Padilla, 2007).
7. ALS piriform bases: (0) normal; (1) reduced (Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
8. PMS nubbin: (0) present; (1) absent (Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
9. PMS aciniform gland spigots: (0) extensive; (1) reduced (Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
10. PLS mesal cylindrical spigot base: (0) same size of the other PLS cylindrical spigots; (1) enlarged (Hormiga et al., 1995; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
11. PLS mesal cylindrical spigot position: (0) central; (1) peripheral (Hormiga et al., 1995; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
12. PLS aggregate flagelliform triad: (0) aggregate spigots apart from flagelliform spigot; (1) distal end of the aggregate spigots embrace the distal end of the flagelliform spigot (Hormiga et al., 1995; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
13. PLS aggregate gland spigots: (0) normal; (1) enlarged (Hormiga et al., 1995; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
14. Cheliceral stridulatory striae: (0) absent; (1) present (Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
15. Male cheliceral distal curvature: (0) fewer than two times clypeus width; (1) more than two times clypeus width (Álvarez-Padilla, 2007).
16. Cheliceral boss: (0) smooth; (1) striated (Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
17. Cheliceral boss striae: (0) few (<20); (1) numerous (>25) (Hormiga et al., 1995; Álvarez-Padilla, 2007).
18. Cheliceral denticles: (0) absent; (1) present (Hormiga et al., 1995; Álvarez-Padilla, 2007).
19. Male cheliceral length: (0) proportionally the same size of the female; (1) distally elongated (Álvarez-Padilla, 2007).
20. Male cheliceral anterior cuticle: (0) like the clypeal area; (1) covered with scales; (2) covered with small protuberances (Álvarez-Padilla, 2007).
21. Cheliceral dorso-mesal macrosetae: (0) like other macrosetae in the chelicerae; (1) thicker and with a base larger than the other cheliceral macrosetae (Álvarez-Padilla, 2007).
22. Lateral eyes of the male: (0) separate; (1) touching (Coddington, 1990; Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Tanikawa, 2001; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
23. PME tapeta: (0) absent; (1) present (Levi, 1980; Coddington, 1990; Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
24. PLE tapeta: (0) absent; (1) present (Levi, 1980; Coddington, 1990; Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
25. Clypeus height: (0) smaller than one AME diameter; (1) equal or larger than one AME diameter; (2) larger than two AME diameters (Levi, 1980; Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Tanikawa, 2001; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
26. Posterior gut caeca: (0) absent; (1) present. Palmgren (1978a, 1978b) was the first to report differences in the anatomy of the intestinal caeca between Araneidae and Tetragnathidae. These differences were used in many of the later phylogenetic treatments including these two groups (Levi, 1980; Hormiga et al., 1995; Griswold et al., 1998; Álvarez-Padilla, 2007).
27. Dorsal femoral trichobothria: (0) present; (1) absent (Levi, 1980; Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Tanikawa, 2001; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
28. Femur IV trichobothria arrangement: (0) one irregular line; (1) two parallel rows (Álvarez-Padilla, 2007).
29. Trichobothria morphology: (0) annulated; (1) smooth; (2) branched (Álvarez-Padilla, 2007).
30. Femur IV trichobothria extension: (0) less than one-third of the femur length; (1) more than one-third of the femur length (Álvarez-Padilla, 2007).

31. Tibia IV: (0) without tufts of setae on the distal end; (1) with tufts of setae on the distal end (Álvarez-Padilla, 2007).
32. Patella-tibia autospasy: (0) absent; (1) present (Hormiga, 1993, 1994; Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
33. Sustentaculum: (0) absent; (1) present (Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
34. Tarsus IV theridiid comb: (0) absent; (1) present (Coddington, 1990; Hormiga et al., 1995; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
35. Size of the male: (0) >0.5 female; (1) <0.4 female (Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
36. Palpal patella macrosetae of the male: (0) one; (1) none; (2) two (Hormiga et al., 1995; Scharff and Coddington, 1997; Tanikawa, 2001; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
37. Male palpal tibial distal margin: (0) smooth; (1) with apophyses (Álvarez-Padilla, 2007).
38. Cymbium apical margin: (0) entire; (1) constricted (Hormiga et al., 1995; Griswold et al., 1998; Álvarez-Padilla, 2007).
39. Cymbium orientation: (0) dorsal; (1) mesal (Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Kuntner, 2006; Álvarez-Padilla, 2007).
40. Cymbial distal margin: (0) smooth; (1) with a long process (Álvarez-Padilla, 2007).
41. Cymbial base: (0) smooth; (1) with a process (Álvarez-Padilla, 2007).
42. Cymbial basal process shape: (0) massive; (1) long spine with cuticle different from cymbium; (2) small, roughly triangular; (3) covered with denticles; (4) slightly protruding and with several spines; (5) short spine with the base enlarged; (6) long triangular spine; (7) short spine on a ridge (Álvarez-Padilla, 2007).
43. Cymbial basal process and paracymbium relative position: (0) basal; (1) distal; (2) paracymbium not originating at the cymbial basal process (Álvarez-Padilla, 2007).
44. Cymbial basal process modifications: (0) cymbial base slightly swollen; (1) short protuberances; (2) one long spine; (3) long apophysis covered with denticles; (4) several spines of variable length (Álvarez-Padilla, 2007).
45. Cymbial basal process position: (0) dorsal; (1) ectal (Álvarez-Padilla, 2007).
46. Cymbial ectal edge median portion: (0) smooth; (1) with a process (Álvarez-Padilla, 2007).
47. Cymbial median process shape: (0) short; (1) long; (2) globular (Álvarez-Padilla, 2007).
48. Cymbial median process macrosetae: (0) none; (1) like the macrosetae on the cymbium; (2) enlarged (Álvarez-Padilla, 2007).
49. Cymbial median process base diameter: (0) gradually increasing diameter toward its base; (1) abruptly enlarged (Álvarez-Padilla, 2007).
50. Paracymbium: (0) absent; (1) integral; (2) intersegmental; (3) articulated (Levi, 1980; Coddington, 1990; Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Álvarez-Padilla, 2007). Paracymbium morphology is also coded in Kuntner (2005, 2006), but only in reference to variation in shape; none of his characters refer to the connection between the cymbium and the paracymbium.
51. Paracymbium distal margin: (0) smooth; (1) with a triangular sclerotized growth (Álvarez-Padilla, 2007).
52. Degree of sclerotization of the paracymbium base: (0) sclerotized like cymbium; (1) less sclerotized (Hormiga et al., 1995; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
53. Paracymbium morphology: (0) short basal structure, hook-shaped; (1) longer than wide and fingerlike; (2) flat and roughly rectangular; (3) U-shaped; (4) long projection of the basal half of the cymbium continuous with the retrolateral margin; (5) flat and roughly triangular; (6) very large and broader than width of cymbium (Hormiga et al., 1995; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
54. Paracymbium apophysis: (0) absent; (1) anterior; (2) folding of margin; (3) basal; (4) several apophyses (Hormiga et al., 1995; Álvarez-Padilla, 2007).
55. Subtegulum and tegulum relative position: (0) subtegulum located under the tegulum; (1) subtegulum ectally displaced (Álvarez-Padilla, 2007).
56. Tegular sclerites: (0) subterminal; (1) apical (Hormiga et al., 1995; Álvarez-Padilla, 2007).
57. Tegulum ventral surface: (0) not enlarged; (1) ventrally enlarged (Álvarez-Padilla, 2007).
58. Sperm reservoir (sperm duct): (0) normal; (1) enlarged (Coddington, 1990; Hormiga et al., 1995; Griswold et al., 1998; Álvarez-Padilla, 2007).
59. Sperm duct: (0) with fewer than four turns; (1) more than four coiled turns (Álvarez-Padilla, 2007).
60. Reservoir course (sperm duct): (0) spiraled; (1) with a switchback (Coddington, 1990; Hormiga et al., 1995; and Tanikawa, 2001; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
61. Median apophysis: (0) present; (1) absent (Coddington, 1990; Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Tanikawa, 2001; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
62. Conductor and embolus: (0) separate; (1) conductor wraps embolus (Coddington, 1990; Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Tanikawa, 2001; Álvarez-Padilla, 2007). Note that Kuntner (2005, 2006) interpreted differently the conductor in "nephilids"; see notes on conductor homology and coding in the character section.
63. Conductor origin: (0) near embolus; (1) ventral margin of the tegulum; (2) center of the tegulum; (3) dorsal margin of the tegulum; (4) tegular rim (Álvarez-Padilla, 2007).
64. Conductor embolus coverage: (0) less than one-third of the embolus; (1) entire; (2) between one-

third and two-thirds of the embolus (Álvarez-Padilla, 2007).
65. Conductor tip: (0) lamelliform and without ornamentations; (1) with several lobes and a distal hook (Álvarez-Padilla, 2007).
66. Conductor apex: (0) straight; (1) curved apically (Álvarez-Padilla, 2007).
67. Sigmoid distal end of the conductor: (0) absent; (1) present (Hormiga et al., 1995; Griswold et al., 1998; Álvarez-Padilla, 2007).
68. Embolus tegulum orientation: (0) parallel; (1) 90° (Hormiga et al., 1995; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
69. Araneid radix: (0) absent; (1) present (Coddington, 1990; Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Álvarez-Padilla, 2007). Radix is differently interpreted by Kuntner (2005, 2006), as he calls radix, or at least accepts as homologs to it all widened emboli bases.
70. Stipes: (0) absent; (1) present (Hormiga et al., 1995; Scharff and Coddington, 1997; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
71. Distal hematodocha: (0) absent; (1) present (Hormiga et al., 1995; Scharff and Coddington, 1997; Álvarez-Padilla, 2007).
72. Metine embolic apophysis: (0) absent; (1) present (Coddington, 1990; Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Tanikawa, 2001; Álvarez-Padilla, 2007).
73. Embolus length: (0) less than twice the embolus base length; (1) more than twice the embolus base length (Álvarez-Padilla, 2007).
74. Embolic basal apophysis attachment: (0) membranous; (1) sclerotized (Álvarez-Padilla, 2007).
75. Embolic basal apophysis shape: (0) several apophyses; (1) single massive sclerite; (2) long and slender; (3) hook-shaped; (4) coiling with embolus; (5) short spine (Álvarez-Padilla, 2007).
76. Embolic apophysis apex: (0) straight; (1) curved (Álvarez-Padilla, 2007).
77. Embolus tegulum membrane: (0) absent; (1) present (Hormiga et al., 1995; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
78. Theridiid tegular apophysis: (0) absent; (1) present (Coddington, 1990; Hormiga et al., 1995; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
79. Epigynum: (0) present; (1) absent (Hormiga et al., 1995; Álvarez-Padilla, 2007).
80. Fertilization ducts: (0) present; (1) absent (Levi, 1980; Coddington, 1990; Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Álvarez-Padilla, 2007).
81. Copulatory openings: (0) divided by a plate; (1) within a sclerotized atrium; (2) within a membranous sac (Álvarez-Padilla, 2007).
82. Fertilization ducts length: (0) less than half the spermatheca length; (1) more than half the spermathecae length (Álvarez-Padilla, 2007).
83. Fertilization ducts path: (0) straight; (2) coiled (Álvarez-Padilla, 2007).
84. Spermathecae: (0) oval; (1) subdivided in two lobes (Álvarez-Padilla, 2007).
85. Spermatheca surface: (0) sclerotized; (1) membranous (Álvarez-Padilla, 2007).
86. Epigynum ventral plate: (0) truncate to gently rounded; (1) with a scape (Álvarez-Padilla, 2007).
87. Copulatory ducts: (0) free between the spermathecae; (1) within a membranous sack (Álvarez-Padilla, 2007).
88. Epigynum tip: (0) smooth; (1) with two invaginations; (2) invaginations rebordered (Álvarez-Padilla, 2007).
89. Epigynal caudal plate: (0) smooth; (1) with distal outgrowths (Álvarez-Padilla, 2007).
90. Epigynal opening shape: (0) like a spiracle; (1) excavated, longer than wide; (2) longer than wide with the anterior edges rounded; (3) protruding; (4) flat; (5) longitudinal atria; (6) excavated wider than long (Álvarez-Padilla, 2007).
91. Fertilization ducts origin: (0) posterior; (1) anterior (Álvarez-Padilla, 2007).
92. Fertilization ducts and spermathecae: (0) separated; (1) ducts coiling around spermathecae (Álvarez-Padilla, 2007).
93. Web posture: (0) extended legs I and II; (1) flexed (Levi, 1980; Coddington, 1990; Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
94. Web architecture: (0) orb; (1) sheet; (2) gum foot (Coddington, 1990; Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al,. 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
95. Hub against substrate: (0) absent; (1) present (Hormiga et al., 1995; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
96. Hub bite-out: (0) absent; (1) present (Coddington, 1990; Hormiga et al., 1995; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
97. Hub: (0) closed; (1) open (Levi, 1980; Coddington, 1990; Hormiga et al., 1995; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
98. Hub loop: no sticky spiral shift: (0) gradual; (1) abrupt (Hormiga et al., 1995; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
99. Radii construction: (0) radii singly attached; (1) radii attached twice (Coddington, 1990; Hormiga et al., 1995; Griswold et al., 1998; Álvarez-Padilla, 2007).
100. Radii construction: (0) radii not cut and reeled; (1) radii cut and reeled (Coddington, 1990; Hormiga et al., 1995; Griswold et al., 1998; Álvarez-Padilla, 2007).
101. Nonsticky spiral: (0) removed from finished web; (1) remains in finished web (Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
102. Nonsticky contact in first sticky spiral construction: (0) present; (1) absent (Coddington, 1990; Hormiga et al., 1995; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
103. Sticky spiral location: (0) oL1; (1) iL1; (2) oL4 (Levi, 1980; Coddington, 1990; Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
104. Wrap-bite attack: (0) present; (1) absent (Coddington, 1990; Hormiga et al., 1995; Griswold et

al., 1998; Kuntner, 2005, 2006; Álvarez-Padilla, 2007).
105. Web frame: (0) two-dimensional; (1) three-dimensional (Coddington, 1990; Griswold et al., 1998; Álvarez-Padilla, 2007).
106. Female carapace: (0) pyriform; (1) oval (Kuntner, 2005, 2006).
107. Posterior eye row: (0) straight to recurved; (1) procurved (Kuntner, 2005, 2006).
108. Female PME: (0) less than one PME diameter apart; (1) one or more than one PME diameter apart (Kuntner, 2005, 2006).
109. Female PLE size: (0) equal or less than PME; (1) larger than PME (Kuntner, 2005, 2006).
110. Female clypeus height: (0) less than one AME diameter; (1) equal or more than one AME diameters; (2) equal or more than two AME diameters (Kuntner, 2005, 2006).
111. Female sternum: (0) longer than wide; (1) as wide or wider than long (Kuntner, 2005, 2006).
112. Sternal slit sensila: (0) present; (1) absent (Kuntner, 2005, 2006).
113. Female sternal tubercle I: (0) absent; (1) present (Kuntner, 2005, 2006).
114. Female sternal tubercle II: (0) absent; (1) present (Kuntner, 2005, 2006).
115. Female sternal tubercle III: (0) absent; (1) present (Kuntner, 2005, 2006).
116. Female sternal tubercle IV: (0) absent; (1) present (Kuntner, 2005, 2006).
117. Female frontal sternal tubercle: (0) absent; (1) present (Kuntner, 2005, 2006).
118. Female chilum: (0) absent: (1) present (Kuntner, 2005, 2006).
119. Female chelicerae: (0) massive; (1) slender (Kuntner, 2005, 2006).
120. Prosomal supercheliceral lobe: (0) present; (1) absent (Kuntner, 2005, 2006).
121. Female first femur: (0) more/less straight; (1) sigmoidal (Kuntner, 2005, 2006).
122. Femoral macrosete: (0) present; (1) absent (Griswold et al., 1998; Kuntner, 2005, 2006).
123. Female anterior abdominal humps: (0) absent; (1) present (Kuntner, 2005, 2006).
124. Female ventromedial sclerotizations: (0) absent; (1) paired sclerotizations (Kuntner, 2005, 2006).
125. Female abdominal sigillae: (0) absent; (1) present. Not as in Kuntner (2005, 2006); see notes in the character section.
126. Female abdomen tip color: (0) no different to the subapical abdomen; (1) paired white dots around spinnerets (Kuntner, 2005, 2006).
127. Female venter light pigmented pattern form: (0) one central light area; (1) transverse line(s); (2) four large spots; (3) numerous spots; (4) longitudinal lines; (5) uniformly colored (Kuntner, 2005, 2006).
128. Epigynal paired sclerotized pocket: (0) absent; (1) present (Kuntner, 2005, 2006).
129. Anterior epigynal area apodemes: (0) absent; (1) present (Kuntner, 2005, 2006).
130. Cuticle anterior to the epigynal area: (0) flat or rounded; (1) depressed (Kuntner, 2005, 2006).
131. Copulatory opening position: (0) caudal; (1) ventral (Kuntner, 2005, 2006).
132. Copulatory opening form: (0) elongated slit openings; (1) rounded openings; (2) transverse groove (Kuntner, 2005, 2006).
133. Copulatory duct morphology: (0) flattened duct (longer than wide, flat); (1) tube (longer than wide, cylindrical); (2) broad attachment to body wall (wider than long) (Kuntner, 2005, 2006).
134. Spermathecae separation: (0) wide (separated more than two widths); (1) small or none (Kuntner, 2005, 2006).
135. Epigynal sclerotized arch: (0) absent; (1) present (Kuntner, 2005, 2006).
136. Female copulatory aperture: (0) no specimens with plugs; (1) emboli plus conductors (Kuntner, 2005, 2006).
137. Male cephalic region: (0) narrower than in female; (1) same proportion to cephalothorax as in female (Kuntner, 2005, 2006).
138. Male clypeus: (0) as in female; (1) more horizontal (Kuntner, 2005, 2006).
139. Male vs. female cheliceral size: (0) same; (1) larger; (2) smaller (Kuntner, 2005, 2006).
140. Male leg II tibial macrosetae: (0) similar to those on tibia I; (1) more robust; (3) absent (Kuntner, 2005, 2006).
141. Male palpal trochanter: (0) short (twice the width or less); (1) long (more than twice the width) (Kuntner, 2005, 2006).
142. Male palpal femoral tubercle: (0) absent; (1) present (Kuntner, 2005, 2006).
143. Cymbium length: (0) short (less than twice the width); (1) long (more than twice the width) (Kuntner, 2005, 2006).
144. Cymbial ectal margin: (0) sclerotized as cymbium; (1) transparent (Kuntner, 2005, 2006).
145. Paracymbium setae: (0) glabrous; (1) with setae (Kuntner, 2006).
146. Paracymbium margin fold: (0) absent; (1) present (Kuntner, 2005, 2006).
147. Male paturon: (0) smooth; (1) with a tubercle (Kuntner, 2005, 2006).
148. Tegulum in ectal view: (0) same size as or larger than subtegulum; (1) smaller than subtegulum (Kuntner, 2005, 2006).
149. Ejaculatory duct: (0) within the entire length of embolus; (1) joins embolus distally of its base (Kuntner, 2005, 2006).
150. Median apophysis: (0) without sperm duct; (1) with a loop of the sperm duct (Kuntner, 2005, 2006).
151. Conductor: (0) absent; (1) present (Kuntner, 2005, 2006).
152. Conductor size: (0) small (less than half bulb volume); (1) large (more than half bulb volume) (Kuntner, 2005, 2006).
153. Embolus (E) length: (0) long (more than 1.5 times cymbium length); (1) medium (0.5–1.5 cymbium length); (2) short (less than half the cymbium length) (Kuntner, 2005, 2006).
154. Embolus hook: (0) smooth; (1) hooked (Kuntner, 2005, 2006).
155. Orb-web angle: (0) horizontal (0–45°); (1) vertical (46–90°) (Kuntner, 2005, 2006).
156. Stabilimentum: (0) absent; (1) present (Kuntner, 2005, 2006).

157. Barrier (three dimensional) web: (0) absent; (1) present (Kuntner 2006).
158. Hub relative position: (0) central; (1) displaced up; (2) displaced down (Kuntner, 2005, 2006).
159. Hub-cup: (0) absent; (1) present (Kuntner, 2005, 2006).
160. Secondary (split) radii: (0) absent; (1) present (Kuntner, 2005, 2006).
161. Tertiary (split) radii: (0) absent; (1) present (Kuntner, 2005, 2006).
162. Wrap-bite silk: (0) dry; (1) sticky (Kuntner, 2005, 2006).
163. Cheliceral clasp: (0) absent; (1) present (Kuntner, 2005, 2006).
164. Bulbus detachment (eunuchs): (0) absent; (1) present (Kuntner, 2005, 2006).
165. Body shake: (0) absent; (1) present (Kuntner, 2005, 2006).
166. Partial web renewal: (0) absent; (1) present (Kuntner, 2005, 2006).
167. Retreat: (0) absent; (1) off-web; (2) in web (Kuntner, 2005, 2006).
168. Retreat form: (0) silken tube; (1) utilization of a leaf (Kuntner, 2005, 2006).
169. Macrosetae on the PLS: (0) absent; (1) present (e.g., figs. 28G, J, 35E).
170. Chelicerae projection: (0) chelicerae not projected (fig. 1A, C); (1) projected.
171. Chelicerae divergence: (0) not divergent (fig. 4E); (1) moderately divergent (fig. 4C); (2) widely divergent (fig. 4D).
172. Cheliceral dorsal tooth: (0) absent; (1) present (figs. 12E, 42E, 53B, D).
173. Chelicerae dorsal tooth position: (0) very close to the fang articulation (fig. 42E); (1) outlying the fang articulation (fig. 9E).
174. Cheliceral fang outgrowth. (0) absent (fig. 38B, F); (1) present (fig. 42B, E).
175. Cymbium/tibia proportion: (0) less than 2.8; (1) more than 2.8.
176. Apical embolus membrane: (0) absent; (1) present (fig. 20B, C).
177. Embolus ventral enlargement: (0) embolus with a conspicuously enlarged portion (figs. 37A, 39E, H); (1) embolus without apparent enlargement (fig. 10B, C).
178. Apical embolus membrane extension: (0) does not reach to the embolus tip (fig. 17A–C); (1) reaches near the embolus tip (fig. 8A, B).
179. Embolus tip turnover: (0) absent (fig. 17A–C); (1) present (figs. 41E, 43G).
180. Embolus basal apophysis: (0) absent; (1) present (fig. 9A, B).
181. Conductor basal apophysis: (0) absent; (1) present (figs. 9A, 13I).
182. Conductor basal apophysis membrane: (0) basal apophysis narrower distally and without or with very small membrane distally (fig. 43G); (1) basal apophysis with a transparent membrane distally (fig. 10C); (2) basal apophysis widened distally and without semitransparent distal age (fig. 17A).
183. Conductor apical apophysis: (0) absent; (1) present (figs. 17A, 27A).
184. Embolus serrated membrane: (0) absent; (1) present (fig. 39A, B, I).
185. MEA prolateral fold: (0) absent (Fig. 41A); (1) present (figs. 25A, 27A).
186. Spermathecae: (0) present; (1) absent (figs. 31D, E, 34B–E).
187. Median sac: (0) absent (figs. 7A, B, 40D, E); (1) present (figs. 7C, D, 34B).
188. Uterus externus connecting with the rest of the female genital apparatus via wide membranous saclike chamber: (0) absent; (1) present (figs. 7A–D, 40D, E).
189. Posterior sac: (0) absent; (1) present (figs. 7A–E, 40D, E).
190. Posterior sac stores sperm: (0) absent; (1) present (figs. 40D, E, 44D, E, J).
191. Distal tubercle of the abdomen (male): (0) absent (fig. 58C); (1) present (fig. 1A–C).
192. Orientation distal tubercle abdomen male: (0) vertical (fig. 1A–C); (1) longitudinal (fig. 63B, C).
193. Basal apophysis tip morphology: (0) continuous (fig. 60C); (1) with outgrowths (fig. 10C).
194. Female fovea pits: (0) absent (fig. 60A–C); (1) present (fig. 60E).

APPENDIX 2
Matrix for Phylogenetic Analysis.

		Characters			
		1	1111111112	2222222223	3333333334
	Taxa	1234567890	1234567890	1234567890	1234567890
1	*Allende longipes* Álvarez-Padilla, 2007	0000000010	110000-001	01111?1---	0000000?0
2	*Allende nigrohumeralis* (F. O. P.-Cambridge 1899)	0000000010	110000-001	01111?1---	0000000?0
3	*Allende patagiatus* (Simon, 1901)	0000000010	110000-001	01111?1---	0000000?0
4	*Allende puyehuensis* (Nicolet, 1849)	0000000010	110000-001	01111?1---	0000000?0
5	*Araneus marmoreus* Clerck, 1757	0010000000	010000-100	0111001---	0010020010
6	*Argiope argentata* (Fabricius, 1775)	0010000000	010000-100	0111101---	0010100010
7	*Azilia affinis* O. P.-Cambridge, 1893	0000000000	100000-010	00000?1---	0000000000
8	*Chrysometa saladito* Levi, 1986	0100000010	100000-001	01111?1---	0000000?0
9	*Chrysometa acinosa* Álvarez-Padilla, 2007	000000??1?	1?0000-001	01111?1---	0000001?0
10	*Chrysometa alajuela* Levi, 1986	0100000010	100000-001	01111?1---	0000000?0
11	*Chrysometa levii* Álvarez-Padilla, 2007	0??000????	???0?0-0?1	01111?1---	???0?001?0
12	*Chrysometa maitae* Álvarez-Padilla, 2007	?00000??1?	1?0??0-0??	0???1?1---	0?00??????
13	*Chrysometa nuboso* Levi, 1986	0100000010	100000-001	01111?1---	0000000?0
14	*Clitaetra episinoides* Simon, 1889	0000000010	1100010100	00000?1---	0000000000
15	*Cyrtognatha atopica*	0100?0????	1?0010-001	01111?0021	0000?00100
16	*Cyrtognatha bella* (O. P.-Cambridge, 1896)	0100?0????	1?0010-0?1	01111?0021	0000?00100
17	*Cyrtognatha bryantae* (Chickering, 1956)	0100000010	1?0010-001	01111?0021	0000000100
18	*Cyrtognatha catia*	0100?0????	1?0010-001	01111?0021	0000?00100
19	*Cyrtognatha eberhardi*	0100?0????	1?0010-001	01111?0021	0000?00100
20	*Cyrtognatha espanola* (Bryant, 1945)	0100000010	1?0010-001	0111110021	0000000100
21	*Cyrtognatha insolita* (Chickering, 1956)	0100000010	1?0010-001	01111?0021	0000000100
22	*Cyrtognatha lepida* (O. P.-Cambridge, 1889)	?100000010	1?00?0-0??	0?11??0021	0000??????
23	*Cyrtognatha leviorum*	0100?0????	1?0010-001	01111?0021	0000?00100
24	*Cyrtognatha morona*	0100?0????	1?0010-001	01111?0021	0000?00100
25	*Cyrtognatha nigrovittata* Keyserling, 1881	0100?0????	1?0010-001	01111?0021	0000?00100
26	*Cyrtognatha orphana*	0100000010	1?0010-001	01111?0021	0000000100
27	*Cyrtognatha pachygnathoides* (O. P.-Cambridge, 1894)	0100000010	1?0010-001	01111?0021	0000000100
28	*Cyrtognatha paradoxa*	0100000010	1?0010-001	01111?0021	0000000100
29	*Cyrtognatha pathetica*	?100000010	1?00?0-0??	0?????0021	0000??????
30	*Cyrtognatha petila*	0100000010	1?0010-001	01111?0021	0000000100
31	*Cyrtognatha quichua*	0100000010	1?0010-001	01111?0021	0000000100
32	*Cyrtognatha rucilla* (Bryant, 1945)	0100000010	1?0010-001	01111?0021	0000000100
33	*Cyrtognatha serrata* Simon, 1897	0100000010	1?0010-001	01111?0021	0000000100
34	*Cyrtognatha simoni* (Bryant, 1940)	0100000010	1?0010-001	01111?0021	0000000100
35	*Cyrtognatha waorani*	0100?0????	1?0010-001	01111?0021	0000?00100
36	*Diphya sp.*	000000??1?	1?0000-002	00001?1---	0000001?0
37	*Dolichognatha pentagona* (Hentz, 1850)	0000000010	100000-012	00000?1---	0000010000
38	*Epeirotypus brevipes* O. P.-Cambridge, 1894	0000001010	10000 - -100	01112?1---	0000010000

APPENDIX 2
(*Continued*)

		Characters			
		1	1111111112	2222222223	3333333334
	Taxa	1234567890	1234567890	1234567890	1234567890
39	*Gasteracantha cancriformis* (Linnaeus, 1758)	0010110000	110?00-102	01110?1---	0000110?0
40	*Glenognatha foxi* (McCook, 1894)	0001000011	100010-001	01012?0010	0000010100
41	*Herennia multipunta* (Doleschall, 1859)	1010000010	1100011100	01101?1---	0010100000
42	*Leucauge venusta* (Walckenaer, 1842)	0100000010	100000-000	1111110121	0000000000
43	*Linyphia triangularis* (Clerck, 1757)	0000001111	100110-000	0111201---	0100000000
44	*Mangora gibberosa* (Hentz, 1847)	001000000?	???000-100	01110?1---	00100000?0
45	*Mecynogea lemniscata* (Walckenaer, 1842)	0010000000	010000-100	01110?1---	00100000?0
46	*Mesida argentiopunctata* (Rainbow, 1916)	010000??1?	1?0000-012	01111?0121	00000000?0
47	*Metabus conacyt* Álvarez-Padilla, 2007	010000??1?	1?0000-000	01111?1---	0000000?0
48	*Metabus debilis* (O. P - Cambridge, 1899)	010000??1?	1?0000-000	01111?1---	0000000?0
49	*Metabus ebanoverde* Álvarez-Padilla, 2007	010000??1?	1?0000-000	01111?1---	0000000?0
50	*Metabus ocellatus* (Keyserling, 1864)	0100000010	100000-000	01111?1---	00000000?0
51	*Meta menardi* (Latreille, 1804)	0010000000	100000-000	0111101---	0000000000
52	*Metellina curtisi* (McCook, 1894)	0000000010	100010-000	01111?1---	0000000000
53	Metine from Australia	000000??1?	1?0000-001	01111?1---	00000000?1
54	*Micrathena gracilis* (Walckenaer, 1805)	001011000?	???000-100	01110?1---	0000100?0
55	*Mollemeta edwardsi* (Simon, 1904)	0000000010	110000-000	01111?1---	0000000?0
56	*Nanometa sp.*	010000??1?	1?0000-000	01111?1---	0000000?0
57	*Nephila clavipes* (Linnaeus, 1767)	1010000010	1100011100	01111?1---	1010100000
58	*Nephilengys malabarensis* (Walckenaer, 1842)	1010000010	1100011100	01101?1---	0010100000
59	*Nesticus cellulanus* (Clerck, 1757)	0010001010	101000-102	0111211---	0001000000
60	*Opadometa sp.*	010000??1?	1?0000-010	01111?0121	1000110?0
61	*Orsinome sarasini* Berland, 1924	000000??1?	1?0000-001	01111?1---	00000000?1
62	*Orsinome sp.*	010000????	1?0010-000	01111?0010	00000000?0
63	*Pachygnatha autumnalis* Marx, 1884	0000000111	100010-000	0101110010	0000010100
64	*Phonognatha graeffei* (Keyserling, 1865)	0010000010	100000-100	01110?1---	0000000000
65	*Pimoa sp.*	0000001111	10010--000	01112?1---	0100000000
66	*Plesiometa argyra* (Walckenaer, 1842)	010000??1?	1?0000-000	11111?0121	00000000?0
67	*Steatoda americana* (Emerton, 1882)	0000001110	101000-002	01112?1---	0001000000
68	*Tetragnatha javana* (Thorell, 1890)	0100000010	100010-000	00111?0010	0000000100
69	*Tetragnatha spDR*	0100000010	100010-000	00111?0010	0000000100
70	*Tetragnatha versicolor* (Walckenaer, 1842)	0100000010	100010-000	0000110010	0000000100
71	*Tylorida striata* (Thorell, 1877)	010000??1?	1?0000-000	01111?0010	0000100?0
72	*Uloborus glomosus* (Walckenaer, 1842)	0000000100	0-000--100	00000?0000	0000000000

APPENDIX 2
(*Continued*)

		Characters			
	Taxa	4444444445 1234567890	5555555556 1234567890	6666666667 1234567890	7777777778 1234567890
1	*Allende longipes* Álvarez-Padilla, 2007	1313112213	1-10010000	1132100000	0100311000
2	*Allende nigrohumeralis* (F. O. P.-Cambridge 1899)	1313111203	1-10010000	1132100000	0100311000
3	*Allende patagiatus* (Simon, 1901)	1313111203	1-10010000	1132100000	0100301000
4	*Allende puyehuensis* (Nicolet, 1849)	1112111213	1-10010000	1132100000	0100301000
5	*Araneus marmoreus* Clerck, 1757	0----0---1	1000000000	0040000011	1100001000
6	*Argiope argentata* (Fabricius, 1775)	0----0---1	0000000000	0040000011	000---1000
7	*Azilia affinis* O. P.-Cambridge, 1893	0----0---1	0000111011	1----0-000	000---1000
8	*Chrysometa saladito* Levi, 1986	1210110003	?-64010000	1132000000	0110401000
9	*Chrysometa acinosa* Álvarez-Padilla, 2007	1110112003	1-10010000	1132000000	0101501000
10	*Chrysometa alajuela* Levi, 1986	1210111103	?-64010000	1132000000	0100401000
11	*Chrysometa levii* Álvarez-Padilla, 2007	1210110003	1-10010000	1132000000	01004010??
12	*Chrysometa maitae* Álvarez-Padilla, 2007	??????????	??????????	?????0????	????????00
13	*Chrysometa nuboso* Levi, 1986	1210111103	?-64010000	1132000000	0100401000
14	*Clitaetra episinoides* Simon, 1889	0----0---1	0122010011	1111000100	001---1000
15	*Cyrtognatha atopica*	0----0---3	1000010100	1122000000	01010010??
16	*Cyrtognatha bella* (O. P.-Cambridge, 1896)	0----0---3	1000010100	1122000000	000---10??
17	*Cyrtognatha bryantae* (Chickering, 1956)	0----0---3	1000010100	1122000000	000---1011
18	*Cyrtognatha catia*	0----0---3	1000010100	1122000000	01010010??
19	*Cyrtognatha eberhardi*	0----0---3	1000010100	1122000000	01010010??
20	*Cyrtognatha espanola* (Bryant, 1945)	0----0---3	1000010100	1122000000	000---1011
21	*Cyrtognatha insolita* (Chickering, 1956)	0----0---3	1000010100	1122000000	0101001011
22	*Cyrtognatha lepida* (O. P.-Cambridge, 1889)	??????????	??????????	??????????	????????11
23	*Cyrtognatha leviorum*	0----0---3	1000010100	1122000000	01010010??
24	*Cyrtognatha morona*	0----0---3	1000010100	1122000000	01010010??
25	*Cyrtognatha nigrovittata* Keyserling, 1881	0----0---3	1000010100	112?000000	01010010??
26	*Cyrtognatha orphana*	0----0---3	1000010100	1122000000	0101001011
27	*Cyrtognatha pachygnathoides* (O. P.-Cambridge, 1894)	0----0---3	1000010100	1122000000	0101001011
28	*Cyrtognatha paradoxa*	0----0---3	1000010100	1122000000	000---1011
29	*Cyrtognatha pathetica*	??????????	??????????	??????????	????????11
30	*Cyrtognatha petila*	0----0---3	1000010100	1122000000	0101001011
31	*Cyrtognatha quichua*	0----0---3	1000010100	1122000000	0101001011
32	*Cyrtognatha rucilla* (Bryant, 1945)	0----0---3	1000010100	1122000000	000---1011
33	*Cyrtognatha serrata* Simon, 1897	0----0---3	1000010100	1122000000	000---1011
34	*Cyrtognatha simoni* (Bryant, 1940)	0----0---3	1000010100	1122000000	000---1011
35	*Cyrtognatha waorani*	0----0---3	1000010100	1122000000	01010010??
36	*Diphya sp.*	172010---1	1001010000	1111000000	000---1000
37	*Dolichognatha pentagona* (Hentz, 1850)	101210---1	0010010001	1132000000	0101201000

APPENDIX 2
(*Continued*)

		Characters			
		4444444445	5555555556	6666666667	7777777778
	Taxa	1234567890	1234567890	1234567890	1234567890
38	*Epeirotypus brevipes* O. P.-Cambridge, 1894	0----0---1	0000001001	0031000000	000---0000
39	*Gasteracantha cancriformis* (Linnaeus, 1758)	0----0---1	0001000000	0040000010	000---1000
40	*Glenognatha foxi* (McCook, 1894)	0----0---3	1-11010100	1121000000	000---1011
41	*Herennia multipunta* (Doleschall, 1859)	0----0---1	0122010011	1111001100	001---1000
42	*Leucauge venusta* (Walckenaer, 1842)	0----0---1	1000111011	1111000000	001---1000
43	*Linyphia triangularis* (Clerck, 1757)	0----0---2	0-30010000	1---00-000	0100001000
44	*Mangora gibberosa* (Hentz, 1847)	0----0---1	1000000000	0040000011	1100001000
45	*Mecynogea lemniscata* (Walckenaer, 1842)	0----0---1	0000000000	0040000011	101---1000
46	*Mesida argentiopunctata* (Rainbow, 1916)	152000---1	0000111011	1111000000	001---1000
47	*Metabus conacyt* Álvarez-Padilla, 2007	0----0---1	0000111011	1111010000	001---1000
48	*Metabus debilis* (O. P - Cambridge, 1899)	0----0---1	0000111011	1111010000	001---1000
49	*Metabus ebanoverde* Álvarez-Padilla, 2007	0----0---1	0000111011	1111010000	001---1000
50	*Metabus ocellatus* (Keyserling, 1864)	162000---1	0000111011	1111010000	001---1000
51	*Meta menardi* (Latreille, 1804)	1001110001	0010010001	1132000000	0101101000
52	*Metellina curtisi* (McCook, 1894)	100110---1	0010010000	1132000000	0101101000
53	Metine from Australia	1424110001	?000010000	1132000000	000---1000
54	*Micrathena gracilis* (Walckenaer, 1805)	0----0---1	0001000000	0040000010	000---1000
55	*Mollemeta edwardsi* (Simon, 1904)	1002110001	0010010000	1130000000	000---1000
56	*Nanometa sp.*	1424110001	?010010000	1132000000	000---1000
57	*Nephila clavipes* (Linnaeus, 1767)	0----0---1	0122010011	1111000100	001---1000
58	*Nephilengys malabarensis* (Walckenaer, 1842)	0----0---1	0122010011	1111001100	001---1000
59	*Nesticus cellulanus* (Clerck, 1757)	1----0---1	0064000001	0040000000	000---0100
60	*Opadometa sp.*	152000---1	1000111001	1111001000	001---1000
61	*Orsinome sarasini* Berland, 1924	1424110001	?010010000	1132000000	000---1000
62	*Orsinome sp.*	172000---1	10001110?1	1111000000	001---1000
63	*Pachygnatha autumnalis* Marx, 1884	0----0---3	1-11010100	1121000000	000---1011
64	*Phonognatha graeffei* (Keyserling, 1865)	0----0---1	0042000000	1101000000	001---1000
65	*Pimoa sp.*	0----1---1	0050000001	00-0000000	000---0000
66	*Plesiometa argyra* (Walckenaer, 1842)	162000---1	1000111001	1111000000	001---1000
67	*Steatoda americana* (Emerton, 1882)	-----0---0	----000000	0041000000	000---0100
68	*Tetragnatha javana* (Thorell, 1890)	0----0---3	0-11010100	1121000000	000---1011
69	*Tetragnatha spDR*	0----0---3	0-11010100	1121000000	000---1011
70	*Tetragnatha versicolor* (Walckenaer, 1842)	0----0---3	0-11010100	1121000000	000---1011
71	*Tylorida striata* (Thorell, 1877)	152000---1	0000111011	1111000000	001---1000
72	*Uloborus glomosus* (Walckenaer, 1842)	0----0---0	----000000	0040000000	000---0000

APPENDIX 2
(*Continued*)

		Characters			
			1	1111111111	1111111111
		8888888889	9999999990	0000000001	1111111112
	Taxa	1234567890	1234567890	1234567890	1234567890
1	*Allende longipes* Álvarez-Padilla, 2007	0000000103	00?00?????	?????00?0?	?????????0?
2	*Allende nigrohumeralis* (F. O. P.-Cambridge 1899)	0000000103	00?00?????	?????00001	1010110000
3	*Allende patagiatus* (Simon, 1901)	0000000213	00?00?????	?????00?0?	?????????0?
4	*Allende puyehuensis* (Nicolet, 1849)	0000000213	00?00?1???	0????00?0?	?????????0?
5	*Araneus marmoreus* Clerck, 1757	0000010003	??10010001	0000000000	0011110100
6	*Argiope argentata* (Fabricius, 1775)	0000000003	0010010001	0000001100	1011100110
7	*Azilia affinis* O. P.-Cambridge, 1893	0000100004	0000010101	0?1?000000	001111?000
8	*Chrysometa saladito* Levi, 1986	0110000004	11?00?1???	0???000?0?	?????????0?
9	*Chrysometa acinosa* Álvarez-Padilla, 2007	0110000004	10?00?1???	0???000?0?	?????????0?
10	*Chrysometa alajuela* Levi, 1986	0110000004	11?00?????	0???000001	1000110000
11	*Chrysometa levii* Álvarez-Padilla, 2007	??????????	??????????	??????????	??????????
12	*Chrysometa maitae* Álvarez-Padilla, 2007	0110000004	10?00?1???	0???000?0?	?????????0?
13	*Chrysometa nuboso* Levi, 1986	0110000004	11?00?????	????000?0?	?????????0?
14	*Clitaetra episinoides* Simon, 1889	0000000004	00?01??1??	????000110	1000000000
15	*Cyrtognatha atopica*	??????????	??????????	??????????	??????????
16	*Cyrtognatha bella* (O. P.-Cambridge, 1896)	??????????	??????????	??????????	??????????
17	*Cyrtognatha bryantae* (Chickering, 1956)	2-----0--0	--?????????	?????00100	1000000000
18	*Cyrtognatha catia*	??????????	???00?1???	0?????????	??????????0
19	*Cyrtognatha eberhardi*	??????????	??????????	??????????	??????????
20	*Cyrtognatha espanola* (Bryant, 1945)	2-----0--0	--000?1???	0???000100	0000000000
21	*Cyrtognatha insolita* (Chickering, 1956)	2-----0--0	--?????????	?????00101	100000000?
22	*Cyrtognatha lepida* (O. P.-Cambridge, 1889)	2-----0--0	--?????????	?????00101	0?0000000?
23	*Cyrtognatha leviorum*	??????????	??????????	??????????	??????????
24	*Cyrtognatha morona*	??????????	??????????	??????????	??????????
25	*Cyrtognatha nigrovittata* Keyserling, 1881	??????????	??????????	??????????	??????????
26	*Cyrtognatha orphana*	2-----0--0	--?????????	?????00101	1?0000000?
27	*Cyrtognatha pachygnathoides* (O. P.-Cambridge, 1894)	2-----0--0	--?????????	?????00101	0000000000
28	*Cyrtognatha paradoxa*	2-----0--0	--?????????	?????00101	0?0000000?
29	*Cyrtognatha pathetica*	2-----0--0	--?????????	?????00100	0?0000000?
30	*Cyrtognatha petila*	2-----0--0	--000?1???	0???000100	0?0000000?
31	*Cyrtognatha quichua*	2-----0--0	--?00?1???	0???000101	0?00000000
32	*Cyrtognatha rucilla* (Bryant, 1945)	2-----0--0	--000?1???	0???000100	0000000000
33	*Cyrtognatha serrata* Simon, 1897	2-----0--0	--?????????	?????00100	0?0000000?
34	*Cyrtognatha simoni* (Bryant, 1940)	2-----0--0	--?????????	?????00100	000000000?
35	*Cyrtognatha waorani*	??????????	??????????	??????????	??????????
36	*Diphya sp.*	0001000004	10?00?1???	0???000001	1010000011

APPENDIX 2
(*Continued*)

		Characters			
			1	1111111111	1111111111
		8888888889	9999999990	0000000001	1111111112
	Taxa	1234567890	1234567890	1234567890	1234567890
37	*Dolichognatha pentagona* (Hentz, 1850)	1100000005	0010010101	011?000010	1000000010
38	*Epeirotypus brevipes* O. P.-Cambridge, 1894	1000000003	??10010101	0111100001	0010000101
39	*Gasteracantha cancriformis* (Linnaeus, 1758)	0000010003	00100?01?1	0?0?010100	0011110100
40	*Glenognatha foxi* (McCook, 1894)	2--00-0--0	--0000-?01	0-1?000101	1000000001
41	*Herennia multipunta* (Doleschall, 1859)	0000000004	0010100010	1?21000101	1011110100
42	*Leucauge venusta* (Walckenaer, 1842)	1110100001	0000011101	0110000101	1010100000
43	*Linyphia triangularis* (Clerck, 1757)	1110000003	0011------	---1100102	0000000011
44	*Mangora gibberosa* (Hentz, 1847)	0000010003	0010010001	000?000000	1011100100
45	*Mecynogea lemniscata* (Walckenaer, 1842)	1000000003	??100?00??	1???101100	0011110110
46	*Mesida argentiopunctata* (Rainbow, 1916)	1110100004	00?00?1???	0???010001	1000000000
47	*Metabus conacyt* Álvarez-Padilla, 2007	1110100001	00?????????	?????00?0?	????????0?
48	*Metabus debilis* (O. P - Cambridge, 1899)	1110100006	00?????????	?????00?0?	????????0?
49	*Metabus ebanoverde* Álvarez-Padilla, 2007	1110100006	00?00?1???	0???000?0?	????????0?
50	*Metabus ocellatus* (Keyserling, 1864)	1110100001	00?00?????	????000101	1010000010
51	*Meta menardi* (Latreille, 1804)	0000000003	0000011101	0110000101	0011111010
52	*Metellina curtisi* (McCook, 1894)	1000000004	0000011???	0???000101	1011110010
53	Metine from Australia	0000001004	00?00?1???	0???000001	1000000010
54	*Micrathena gracilis* (Walckenaer, 1805)	0000010003	??100?11?1	0?0?000101	0011010100
55	*Mollemeta edwardsi* (Simon, 1904)	0000000004	00?01?00??	0???000101	0000010100
56	*Nanometa sp.*	1000001004	00?00?1???	0???000001	1000000000
57	*Nephila clavipes* (Linnaeus, 1767)	0000000005	0010000010	1?21010101	1011101100
58	*Nephilengys malabarensis* (Walckenaer, 1842)	0000000004	0010100010	1121010101	0011100100
59	*Nesticus cellulanus* (Clerck, 1757)	0000001003	1012------	---?101102	0000000111
60	*Opadometa sp.*	1100100004	00?00?1???	0???000101	1011110100
61	*Orsinome sarasini* Berland, 1924	0000001003	00?????????	?????00001	1011110010
62	*Orsinome sp.*	1000100004	00?00?1???	0???000001	1010110110
63	*Pachygnatha autumnalis* Marx, 1884	2--00-0--0	--?0011???	????000101	0000000011
64	*Phonognatha graeffei* (Keyserling, 1865)	0000000004	0010100000?	1021010100	0010110100
65	*Pimoa sp.*	0000000003	1011------	---1100002	?100000001
66	*Plesiometa argyra* (Walckenaer, 1842)	0000100003	00?00?1???	????000101	0010100000
67	*Steatoda americana* (Emerton, 1882)	0000000004	0012------	---1100002	1000000111
68	*Tetragnatha javana* (Thorell, 1890)	2--??-0--0	--?????????	?????00102	0000000010
69	*Tetragnatha spDR*	2--10-0--0	--?????????	?????00102	0000000010
70	*Tetragnatha versicolor* (Walckenaer, 1842)	2--10-0--0	--00011101	0111000101	0000000010
71	*Tylorida striata* (Thorell, 1877)	1110100004	00?00?1???	0???000001	1010110000
72	*Uloborus glomosus* (Walckenaer, 1842)	0110100003	000000--00	0000000100	0000000000

APPENDIX 2
(*Continued*)

	Taxa	Characters 1111111111 2222222223 1234567890	1111111111 3333333334 1234567890	1111111111 4444444445 1234567890	1111111111 5555555556 1234567890
1	*Allende longipes* Álvarez-Padilla, 2007	???????0??	002100??0?	1???1????-	1120??????
2	*Allende nigrohumeralis* (F. O. P.-Cambridge 1899)	0001100001	0021001?00	100010001-	1120??????
3	*Allende patagiatus* (Simon, 1901)	???????0??	002100??0?	1???1????-	1120??????
4	*Allende puyehuensis* (Nicolet, 1849)	???????0??	002100??0?	1???1????-	1120000000
5	*Araneus marmoreus* Clerck, 1757	0001114001	11?1010121	0111001000	1020100000
6	*Argiope argentata* (Fabricius, 1775)	0011101101	1121011120	0001000000	1011110000
7	*Azilia affinis* O. P.-Cambridge, 1893	0000100000	0111001?00	100110000-	0-20000000
8	*Chrysometa saladito* Levi, 1986	???????0??	002100??1?	????1??0?-	11101?????
9	*Chrysometa acinosa* Álvarez-Padilla, 2007	???????0??	102100??1?	????1??0?-	11201????0
10	*Chrysometa alajuela* Levi, 1986	0000105000	0?21000?10	000110001-	1110100000
11	*Chrysometa levii* Álvarez-Padilla, 2007	??????????	????????1?	????1??0?-	11101?????
12	*Chrysometa maitae* Álvarez-Padilla, 2007	???????0??	102100????	???????0??	????1?????
13	*Chrysometa nuboso* Levi, 1986	???????0??	002100??1?	????1??0?-	11101?????
14	*Clitaetra episinoides* Simon, 1889	0000114000	0011001000	000111?00-	1100100???
15	*Cyrtognatha atopica*	??????????	???--????0	101010000-	1110??????
16	*Cyrtognatha bella* (O. P.-Cambridge, 1896)	??????????	???--????0	101010000-	1110??????
17	*Cyrtognatha bryantae* (Chickering, 1956)	0010114--0	020--01010	101010000-	1010??????
18	*Cyrtognatha catia*	??????????	???--????0	101010000-	1110000000
19	*Cyrtognatha eberhardi*	??????????	???--????0	101010000-	1110??????
20	*Cyrtognatha espanola* (Bryant, 1945)	0010114--0	020--01010	101010000-	1010?00000
21	*Cyrtognatha insolita* (Chickering, 1956)	0010???--0	020--01010	101010000-	1110??????
22	*Cyrtognatha lepida* (O. P.-Cambridge, 1889)	0010114--0	020--0????	?????????-	??????????
23	*Cyrtognatha leviorum*	??????????	???--????0	101010000-	1110??????
24	*Cyrtognatha morona*	??????????	???--????0	101010000-	1110??????
25	*Cyrtognatha nigrovittata* Keyserling, 1881	??????????	???--????0	101010000-	1110??????
26	*Cyrtognatha orphana*	00101??--0	020--01010	101010000-	1110??????
27	*Cyrtognatha pachygnathoides* (O. P.-Cambridge, 1894)	0010104--0	020--01010	101010000-	1110??????
28	*Cyrtognatha paradoxa*	0010114--0	020--01010	101010000-	1110??????
29	*Cyrtognatha pathetica*	001?1??--0	020--0????	?????????-	??????????
30	*Cyrtognatha petila*	0010114--0	020--01010	101010000-	1110?00000
31	*Cyrtognatha quichua*	00101??--0	020--01010	101010000-	1110000000
32	*Cyrtognatha rucilla* (Bryant, 1945)	0010114--0	020--01010	101010000-	1010000000
33	*Cyrtognatha serrata* Simon, 1897	001011?--0	020--01010	101010000-	1110??????
34	*Cyrtognatha simoni* (Bryant, 1940)	0010114--0	020--01010	101010000-	1010??????
35	*Cyrtognatha waorani*	??????????	???--????0	101010000-	1110??????
36	*Diphya sp.*	0000114000	11?1001?10	000010100-	1110??????

APPENDIX 2
(*Continued*)

		Characters			
		1111111111	1111111111	1111111111	1111111111
		2222222223	3333333334	4444444445	5555555556
	Taxa	1234567890	1234567890	1234567890	1234567890
37	*Dolichognatha pentagona* (Hentz, 1850)	0010114001	0010001?10	001110100-	1120000000
38	*Epeirotypus brevipes* O. P.-Cambridge, 1894	0000105000	0211001020	0001000000	1110100000
39	*Gasteracantha cancriformis* (Linnaeus, 1758)	0101105001	00?1001?00	000100?000	10?0100000
40	*Glenognatha foxi* (McCook, 1894)	0?001150-0	1210-01010	101010100-	1010000000
41	*Herennia multipunta* (Doleschall, 1859)	0011110111	1111110100	000111000-	110110011?
42	*Leucauge venusta* (Walckenaer, 1842)	0000110000	1111001000	100010000-	1110001000
43	*Linyphia triangularis* (Clerck, 1757)	0001105000	0110001010	100110100-	0-00--1---
44	*Mangora gibberosa* (Hentz, 1847)	0000115000	00?1001?21	0101000000	1020100000
45	*Mecynogea lemniscata* (Walckenaer, 1842)	0010114001	00?1001?00	0001000000	1010001000
46	*Mesida argentiopunctata* (Rainbow, 1916)	0001104000	11?1001?10	100110100-	1110??0000
47	*Metabus conacyt* Álvarez-Padilla, 2007	0??????0??	101100??0?	????1????-	1110??????
48	*Metabus debilis* (O. P - Cambridge, 1899)	0??????0??	101100??0?	????1????-	1110??????
49	*Metabus ebanoverde* Álvarez-Padilla, 2007	0??????0??	101100??0?	????1????-	1110??????
50	*Metabus ocellatus* (Keyserling, 1864)	0000104001	1011001?00	100110000-	111000?000
51	*Meta menardi* (Latreille, 1804)	0001114001	0020001000	100010010-	1120100000
52	*Metellina curtisi* (McCook, 1894)	0000114000	0020001?10	001110000-	1120100000
53	Metine from Australia	0001104100	11?1001?00	100110100-	1110?00000
54	*Micrathena gracilis* (Walckenaer, 1805)	0101105001	01?1001?00	0001000000	1010100000
55	*Mollemeta edwardsi* (Simon, 1904)	0001104101	01?1001?00	100010000-	1110100000
56	*Nanometa sp.*	0100004000	11?1011?00	000010000-	1110000000
57	*Nephila clavipes* (Linnaeus, 1767)	0001110011	0001010110	000111000-	1100111101
58	*Nephilengys malabarensis* (Walckenaer, 1842)	0001113001	1111110110	000111000-	1100101111
59	*Nesticus cellulanus* (Clerck, 1757)	0100000000	0211001002	0001101001	1020--1---
60	*Opadometa sp.*	0001114000	1011001?10	101110000-	1110100000
61	*Orsinome sarasini* Berland, 1924	00001041??	11?1001?00	100010000-	1110??????
62	*Orsinome sp.*	0001104001	11?1001?10	101110000-	1110000000
63	*Pachygnatha autumnalis* Marx, 1884	0100105--0	1200-01010	001010?00-	1110------
64	*Phonognatha graeffei* (Keyserling, 1865)	1011104000	1121011010	001000100-	1110101101
65	*Pimoa sp.*	000010?000	1111001000	000110000-	1020--1---
66	*Plesiometa argyra* (Walckenaer, 1842)	0001114100	1111001?00	100110100-	1110001000
67	*Steatoda americana* (Emerton, 1882)	0101105000	0211001002	0000--0001	1110--1---
68	*Tetragnatha javana* (Thorell, 1890)	00?????--?	02??-01010	101010?00-	1110??????
69	*Tetragnatha spDR*	00?????--?	0201-01010	101010?00-	1110000000
70	*Tetragnatha versicolor* (Walckenaer, 1842)	0000114--0	0201-01010	101010100-	1110000000
71	*Tylorida striata* (Thorell, 1877)	0000105000	11?1001?00	100110000-	1010000000
72	*Uloborus glomosus* (Walckenaer, 1842)	0000014000	0110001100	0100--0000	1020010000

APPENDIX 2
(*Continued*)

	Taxa	Characters			
		1111111111 6666666667 1234567890	1111111111 7777777778 1234567890	1111111111 8888888889 1234567890	1111 9999 1234
1	*Allende longipes* Álvarez-Padilla, 2007	???0?0??00	00-0?00-00	0-0?000000	0-?0
2	*Allende nigrohumeralis* (F. O. P.-Cambridge 1899)	???0?0??00	00-0?00-00	0-00000000	0-?0
3	*Allende patagiatus* (Simon, 1901)	???0?0??00	00-0?00-00	0-0?000000	0-?0
4	*Allende puyehuensis* (Nicolet, 1849)	0??0?0??00	00-0000-00	0-0?000000	0-?0
5	*Araneus marmoreus* Clerck, 1757	0000001000	00-?000-00	0-0?-00000	0--0
6	*Argiope argentata* (Fabricius, 1775)	0000100-00	00-?100-00	0-0?-00000	0--0
7	*Azilia affinis* O. P.-Cambridge, 1893	0??0??1000	00-?000-00	0-00-00000	0-?1
8	*Chrysometa saladito* Levi, 1986	???0?0??00	00-0?0??00	0-0?000000	0--0
9	*Chrysometa acinosa* Álvarez-Padilla, 2007	0??0?0??00	00-0?0??00	0-0?000000	0--0
10	*Chrysometa alajuela* Levi, 1986	0??0?01000	00-0000-00	0-00000000	0--0
11	*Chrysometa levii* Álvarez-Padilla, 2007	???0?0???0	00-0?0??00	0-0?0?????	0--?
12	*Chrysometa maitae* Álvarez-Padilla, 2007	?????0??0?	??????????	?????00000	0-?0
13	*Chrysometa nuboso* Levi, 1986	???0?0??00	00-0?0??00	0-0?000000	?--0
14	*Clitaetra episinoides* Simon, 1889	???0????00	00-??00-00	0-0?-00000	0--0
15	*Cyrtognatha atopica*	???0?0??10	2111100-01	11100?????	111?
16	*Cyrtognatha bella* (O. P.-Cambridge, 1896)	???0?0??10	2101111100	11100?????	0-0?
17	*Cyrtognatha bryantae* (Chickering, 1956)	???0?0??10	2101111000	1010010111	0-00
18	*Cyrtognatha catia*	0??0?00-10	1101110000	10101?????	100?
19	*Cyrtognatha eberhardi*	???0?0??10	2111110001	11100?????	111?
20	*Cyrtognatha espanola* (Bryant, 1945)	0??0?00-10	1100101-10	1010011111	0-00
21	*Cyrtognatha insolita* (Chickering, 1956)	???0?0??10	2110011100	1011010111	0-00
22	*Cyrtognatha lepida* (O. P.-Cambridge, 1889)	?????0???1?	??????????	?????10111	????
23	*Cyrtognatha leviorum*	???0?0??10	1101011100	12100?????	0-1?
24	*Cyrtognatha morona*	???0?0??10	2111111101	10100?????	0-??
25	*Cyrtognatha nigrovittata* Keyserling, 1881	???0?0??10	2111111100	11110?????	110?
26	*Cyrtognatha orphana*	???0?0??10	2101111000	1111010111	0-0?
27	*Cyrtognatha pachygnathoides* (O. P.-Cambridge, 1894)	???0?0??10	1100010010	1010111111	1000
28	*Cyrtognatha paradoxa*	???0?0??10	2110010100	1210010111	0-1?
29	*Cyrtognatha pathetica*	?????0???1?	??????????	?????10111	????
30	*Cyrtognatha petila*	0??0?0??10	1110011100	1111010111	0-0?
31	*Cyrtognatha quichua*	0??0?0??10	1101010100	1010110111	100?
32	*Cyrtognatha rucilla* (Bryant, 1945)	0??0?00-10	1101001-10	1010011111	0-00
33	*Cyrtognatha serrata* Simon, 1897	???0?0??10	1101001-10	1010011111	0-0?
34	*Cyrtognatha simoni* (Bryant, 1940)	???0?0??10	1101101-10	1010011111	0-00
35	*Cyrtognatha waorani*	???0?0??10	2101111100	12100?????	111?
36	*Diphya sp.*	???0????00	00-0000-00	0-00-00000	0--0

APPENDIX 2
(*Continued*)

	Taxa	Characters			
		1111111111 6666666667 1234567890	1111111111 7777777778 1234567890	1111111111 8888888889 1234567890	1111 9999 1234
37	*Dolichognatha pentagona* (Hentz, 1850)	0??0??1000	0110000-00	0-00000000	0--0
38	*Epeirotypus brevipes* O. P.-Cambridge, 1894	0??0000-00	00-?10??00	0-0?-00000	0--0
39	*Gasteracantha cancriformis* (Linnaeus, 1758)	0??0?00-00	00-??0??00	0-0?-00000	0--0
40	*Glenognatha foxi* (McCook, 1894)	0??0?00-00	1110100-00	0-00-00100	0--0
41	*Herennia multipunta* (Doleschall, 1859)	???1??2000	00-??00-00	0-00-00000	0--0
42	*Leucauge venusta* (Walckenaer, 1842)	0010000-00	00-0000-00	0-00-00000	0--1
43	*Linyphia triangularis* (Clerck, 1757)	-??0010-00	00-0100-00	0-00-00000	0--0
44	*Mangora gibberosa* (Hentz, 1847)	0??0?00-00	00-0100-00	0-00-00000	0--0
45	*Mecynogea lemniscata* (Walckenaer, 1842)	0??0????00	00-010?-00	0-00-00000	0--0
46	*Mesida argentiopunctata* (Rainbow, 1916)	0??0?00-00	00-0100-00	0-00-00000	11-1
47	*Metabus conacyt* Álvarez-Padilla, 2007	???0????00	00-0?00-00	0-00-00000	0--?
48	*Metabus debilis* (O. P - Cambridge, 1899)	???0????00	00-0?00-00	0-00-00000	0--?
49	*Metabus ebanoverde* Álvarez-Padilla, 2007	???0??1000	00-0?00-00	0-00-00000	0--?
50	*Metabus ocellatus* (Keyserling, 1864)	0??0????00	00-0000-00	0-00-00000	0--1
51	*Meta menardi* (Latreille, 1804)	0000000-00	00-?000-00	0-00000000	0--0
52	*Metellina curtisi* (McCook, 1894)	0??0?00-00	00-0000-00	0-0?000000	0--0
53	Metine from Australia	0??0?0??00	00-0000-00	0-00-00000	0--0
54	*Micrathena gracilis* (Walckenaer, 1805)	0??0?00-00	00-?100?00	0-00-00000	0--0
55	*Mollemeta edwardsi* (Simon, 1904)	0??0????00	00-?00?-00	0-0?-00000	0--0
56	*Nanometa sp.*	0??0?00-00	00-0000-00	0-00-00000	0--0
57	*Nephila clavipes* (Linnaeus, 1767)	1?00110-00	00-?100-00	0-00-00000	0--0
58	*Nephilengys malabarensis* (Walckenaer, 1842)	1?01??1000	00-?100-00	0-00-00000	0--0
59	*Nesticus cellulanus* (Clerck, 1757)	-10001??00	0????0??00	0-0?-00000	0--0
60	*Opadometa sp.*	0??0?0??00	0????0??00	0-0?-00000	0--?
61	*Orsinome sarasini* Berland, 1924	???0????00	00-?00?-00	0-0?-00000	0--0
62	*Orsinome sp.*	0??0?0??00	00-0100-00	0-00-00000	0--1
63	*Pachygnatha autumnalis* Marx, 1884	-??0?---00	10-0100-00	0-00-00100	0--0
64	*Phonognatha graeffei* (Keyserling, 1865)	1??0002100	00-0000-00	0-00-00000	0--0
65	*Pimoa sp.*	-??0?10-00	?????0??00	0-0?-00000	0--0
66	*Plesiometa argyra* (Walckenaer, 1842)	0??0?00-00	00-0000-00	0-00-00000	0--1
67	*Steatoda americana* (Emerton, 1882)	-1?0010-00	00-0100-00	0-00-00000	0--0
68	*Tetragnatha javana* (Thorell, 1890)	???0????01	1110000-00	0-00-00000	11-1
69	*Tetragnatha spDR*	0??0?00-01	1110000-00	0-00-00110	11-1
70	*Tetragnatha versicolor* (Walckenaer, 1842)	0?10000-01	2110000-00	0-00-00110	0--1
71	*Tylorida striata* (Thorell, 1877)	0??0?0??00	00-0100-00	0-0?-00000	0--1
72	*Uloborus glomosus* (Walckenaer, 1842)	0??0010-00	00-0100-00	0-00-00000	0--0